PARASITOLOGY

PARASITOLOGY

(Founded by G. H. F. Nuttall, F.R.S.)

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VOLUME 51. 1961

CAMBRIDGE
AT THE UNIVERSITY PRESS
1961

PUBLISHED BY
THE SYNDICS OF THE UNIVERSITY PRESS
Bentley House, 200 Euston Road, London, N.W.1
American Branch: 32 East 57th Street, New York 22, N.Y.

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)

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Parasitology (1961), **51**, 1–109
Printed in Great Britain

A list of the parasitic Protozoa, Helminths and Arthropoda recorded from species of the Family Anatidae (Ducks, Geese and Swans)

By GEOFFREY LAPAGE
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(*Received* 9 *May* 1960)

The following list, compiled during my tenure of a grant given by the Nuffield Foundation to the Wildfowl Trust, Slimbridge, Gloucestershire, records species of Protozoa, helminths and Arthropoda found in anatid birds, either by the authors of the papers listed in the References, or by others to whose work these authors refer. It will be seen that there are, after the names of all the parasites, numbers which indicate, by reference to the corresponding numbers in the References, the authors and publications in which the species concerned are recorded. Thus *Cotylurus brevis* (142, 145*) means that this trematode was recorded from *Aix galericulata*, the Mandarin Duck, by Dubois (1953) and that Dubois & Rausch (1950*a*) reported an experimental infection of this duck with it.

The references given do not include text-books of parasitology, because these text-books are readily available in most libraries, and to quote the host lists in them would be merely to repeat information already present in this list. It will be noticed also that some of the authors quoted in the References, such as, to name outstanding examples, Fuhrmann, Lühe, Joyeux & Baer, Gower, Skrjabin, Chester Hughes, have already published valuable host lists of helminths parasitic in anatid and other birds; that Coatney, and Coatney & Roudabush, have respectively published host indexes of the protozoan genera *Leucocytozoon* and *Haemoproteus*; while Thompson and Hopkins & Clay and Zumpt & Till have published host lists of the parasitic Mallophaga and mites. My task has been made much easier by the incorporation of these earlier lists in the list here presented. It should be noted further that, whenever an author quoted has recorded, not only species found by himself, but also others found by other authors, I have, in some instances, recorded here both the publication in which the original finding of the species was recorded and also subsequent references to it, but that, in other instances, in order to reduce the length of the list, only one of these two Records has been included. So far as has been possible, experimental infections have been differentiated in the References from natural ones by adding a * to the numbers which refer to experimental infections.

Certain difficulties are inevitably encountered in the compilation of a list such as this, and one of the most important of them is the fact that the confusion in the synonymy of the species of parasitic animals is equalled, if it is not exceeded, by the confusion in the synonymy of the species of anatid hosts. I have not been able to discuss the synonyms of either the hosts or the parasites because:

(*a*) An adequate discussion of them, even if I were competent to undertake it, would occupy far more space than is available.

(*b*) Other authors, whose publications are quoted in the References, have discussed the synonymies of the parasitic species much more competently than I can. The fact that they do not always agree only makes the task more difficult for me. It will be noted, however, that I have given, in this list, not only the modern names of parasites, so far, at any rate, as these are generally accepted, but also earlier names, now discarded. One reason for doing this is that recent text-books and research papers do not always give old names that have been suppressed, so that the modern reader, unless he is well versed in the intricacies of synonymy, often does not recognize, when he reads the earlier publications, certain modern species under their earlier names.

(*c*) So far as the synonymies of the anatid hosts are concerned, I have adopted the names of these hosts given by Peter Scott in his *A Coloured Key to the Wildfowl of the World* (1957, The Wildfowl Trust, Slimbridge, Gloucestershire). One of my chief difficulties, however, has been to identify the genus, species and, still more difficult, the subspecies, of bird in which the parasites have been found, because frequently the author has not precisely determined the species or subspecies and often, when the publication has been an early one, it has been difficult to be certain that even the genus has been correctly interpreted. In a few instances, in fact, I have not been able to identify the bird host at all and have therefore listed it under the name given by the author. In many instances, however, by consulting taxonomic lists of birds, such as those published by Peters, the British Museum, Delacour and others, this kind of difficulty has been overcome.

To illustrate the difficulty encountered in identifying the genus of bird involved, the genus *Anas* may be quoted. This genus has many synonyms, some of which, given in the earlier literature, refer to the modern genus *Anas*, while others do not. Thus *Spatula clypeata* is clearly the modern *Anas clypeata*, though it is not so readily realized that *A. obscura* is *A. platyrhynchos fulvigula* and that this subspecies has been, until recently, called *A. fulvigula*. All these names, and others I need not mention, have been given to the bird known as the Florida Duck. If we extend our inquiries further we find that the generic name *Anas* may, in the earlier literature, refer, not to the modern genus *Anas* at all, but to genera as different from *Anas*, and from one another, as *Aythya*, *Bucephala*, *Melanitta*, *Histrionicus* and others. Another modern genus that gives difficulty is *Aythya*, some species of which were formerly called *Nyroca*, a name which also refers in some of the earlier literature to other modern genera. Thus *Nyroca hyemalis* is nowadays known as *Clangula hyemalis*, the Old Squaw, which was formerly also known as *Harelda glacialis*. Similarly, some species of the modern genus *Bucephala* were formerly known as species of *Anas*, *Clangula*, *Glaucion* or *Glaucionetta*.

Added, however, to this kind of difficulty in identifying the genus of anatid bird in question is the greater difficulty of finding out which subspecies of the genus is concerned. Thus '*Somateria mollissima*', found in the earlier literature, may have referred to any one of the five subspecies of this genus listed by Scott and, although the locality in which the bird was found does give, when it is clearly

stated, a clue to the subspecies to which it probably belonged, the locality in which a single bird has been found does not, especially if it be a migratory bird accustomed to fly from one continent to another, help very much to identify it with certainty. The locality, moreover, has often been stated by earlier authors so vaguely that it is useless even as a clue. This kind of difficulty is further increased when the bird in question has been kept in a Zoological Garden, or has been a dead bird preserved in a Museum Collection, without, as sometimes has happened, a precise identification of it when it was originally preserved.

I have therefore, whenever this kind of difficulty has arisen, adopted the rule of recording the parasites found under the host-name of what I have considered to be the most likely species or subspecies involved. It is possible, of course, that this may have led to errors so far as subspecies are concerned, but much study of the synonymies of the birds has made it likely that errors of this kind will be found to be errors only in the interpretation of the subspecies.

In the References the English versions of the names of Russian, Polish, Turkish, Chinese and Japanese authors, and also the abbreviations of the titles of the journals quoted, are those used by *The Index Catalogue of Medical and Veterinary Zoology* and I am glad to have this opportunity of acknowledging my great debt to all those who are responsible for this remarkable and invaluable publication. I am also greatly indebted to the editor and staff of *Helminthological Abstracts*, from which a large number of the references have been collected, so that the papers to which they refer could be consulted. The bibliographies in these papers, some of which are extensive, have provided many other references.

I had hoped to add to the list some comments or deductions which may be made from it, but unfortunately space is not available for these here. All I can do is to indicate briefly the following rather obvious conclusions:

(1) So far as helminth parasites are concerned, most of those that infect anatid birds enter the birds with food through the mouth, so that the infection of the birds with them depends on the habits of the bird host and on the food that it selects. Thus snail-eaters are likely to acquire trematode parasites, whose infective phases are parasitic in snails. When, therefore, a large number of different species of trematodes have been recorded from any particular anatid bird, we may conclude that this bird is a snail-eater and that its geographical distribution and habits bring it into contact with the snail-hosts of the trematodes that have been recorded from it. Because cestodes also are acquired by eating the hosts of their infective phases, similar conclusions may be drawn with regard to them. Infections with nematodes will also be related to the feeding habits of the birds, with the exception of infections with microfilarial larvae of Filarioid nematodes, which are transmitted to the birds by blood-sucking insects, so that infection with these is governed by factors which govern infections, transmitted in a similar way, with the protozoan parasites of the blood.

(2) The protozoan parasites can be divided into the Coccidia, which are acquired by eating the oocysts, and the blood parasites (*Haemoproteus*, *Leucocytozoon* and *Trypanosoma*) which must be transmitted to the birds by blood-sucking mosquitoes, black flies and midges.

Because the oocysts of Coccidia are passed out in the faeces of their hosts and are not likely to survive for long periods outside the host, it seems likely that they will be most commonly acquired in places in which the faeces of their hosts are abundant and are relatively sheltered from climatic effects which will kill the oocysts. One would expect, therefore, to find Coccidia most commonly in anatid birds whose habits lead them to congregate, at one or more periods of each year, in breeding grounds, wintering places or other relatively restricted areas, in which infections with these parasites will be most readily picked up. For similar reasons most nematode infections, which are transmitted by infective phases developing in or near the faeces of the birds, will be commoner in birds which congregate in this manner.

Infections with the blood-parasites, on the other hand, which can only be acquired by the bites of adult blood-sucking mosquitoes, black flies or midges, will only be found in anatid birds whose habits lead them to give, if only for a few moments, these blood-sucking insects the opportunity to suck their blood. Because these insects are adult and feed actively only during the summer and, in some instances, the early autumn, and because they cannot fly far away from the land or the area in which they emerged from the pupal stage, we may expect that these blood parasites will be commoner in anatid birds which either spend the greater part of their lives in relatively close contact with the land to which the insects are closely tied, or visit, if only for short periods during their migrations, the areas of land in which the infected insects are present. A correlation will therefore exist between the geographical distribution and ecology of the blood-sucking insect hosts and that of the anatid birds, due regard being given to the migrations, often extensive, in which the anatid birds indulge.

Account must also be taken, when these protozoan infections are being considered, not only of the seasonal appearance of the insect hosts, but also of the seasonal, and even of the daily, variations in numbers of the blood parasites in the birds. The occurrence of these seasonal and daily variations of the numbers of the blood parasites in the birds has been well established by several workers, and it is also known that infection of either the insect or the vertebrate host can only occur when there are sufficient numbers of the blood parasites to enter either of these hosts. If, therefore, a suitable insect host sucks blood from an infected anatid bird at a time when there is, in the blood of the bird, a low seasonal or daily incidence in the numbers of the parasites, it may happen that the insect does not become infected and is therefore unable to transmit the infection to other birds. It may follow, also, that the insect, for one reason or another, is unable, when it sucks the bird's blood, to transmit to it sufficient numbers of the blood parasites to establish an infection in that bird. If, however, the anatid bird lands, shall we say, during a long migration, in an exhausted and insufficiently nourished condition, in an area in which the insect hosts are present, and are perhaps, as they may be in the autumn, when these long migrations may occur, hungry and ready to take up as much bird blood as they can, then the transmission by the infected insect of only a relatively few blood parasites may suffice to establish, in an exhausted and ill-nourished bird, an infection which may be the source of the infection of other insects and, consequently, of other birds. It will be clear, there-

fore, that several factors, most of them at present insufficiently understood, operate in controlling the incidence of these blood parasites in the birds.

Along these lines, indeed, much more could be written about the factors which may influence the incidence, not only of protozoan, but also of the helminth and ectoparasitic species recorded in this list. The ectoparasitic species (lice, fleas, ticks and mites) seem especially to require much further investigation and the further study of them might, as, indeed, the further study of all these parasites might, throw light, not only on the habits and general biology of the birds, but also on the phylogeny and speciation of the anatid birds in general.

I had hoped, if space had been available, to add to the list here given, a companion list of the names of the parasites showing the hosts from which each parasite has been recorded; but it will not, perhaps, be difficult for the reader to pick out, from the list as it is, any information of this kind that he may require. The list does not, as has been indicated above, claim to be complete, but it does, so far as I know at present, contain the majority of the known, recorded species, either under the names originally given to them, or under synonyms of these, and I hope that the list will therefore be useful, not only to those who are interested in the biology and ecology of anatid birds and in any light that may be thrown on these by the study of the parasites, but also to systematists.

All the references listed have been entered on Cope-Chatterson cards, which have been punched in such a manner that, by using the key card provided and passing a needle through the appropriate holes in this and the other cards, all the papers can be selected which relate to:

(1) Each genus of anatid bird, i.e. *Anas*, *Aythya*, *Branta*, etc.; and also such categories as 'domestic duck', 'domestic goose', and 'unidentified birds'.

(2) Each zoological Class of parasites, i.e. Protozoa, Trematoda, Cestoda, Arthropoda, etc.

(3) Experimental infections.

(4) Authors, according to the initials of their surnames.

These cards will be sent, together with a certain number of reprints of some of the papers listed in the References, to the Wildfowl Trust, Slimbridge, Gloucestershire, where the cards and reprints may be consulted.

I am glad to have this opportunity of thanking the Nuffield Foundation for the grant which made it possible to compile this list, and the Wildfowl Trust under whose auspices the work was done. I am grateful also to my wife for the help she has given in dealing with the mass of paper involved in the preparation of the list for the printer, a task which has been in many ways more troublesome than the compilation of the cards or the reading of the many publications consulted. I must thank, too, the Director and Staff of the Commonwealth Bureau of Helminthology, The White House, 103 St Peter's Street, St Albans, for the constant help and encouragement they have given, and also the librarians, both here in Cambridge and elsewhere, for a great deal of help. The work has further been lightened by the skill and care of the typists who have helped to prepare the manuscript, and Miss P. K. A. Seamer, of the Molteno Institute, Cambridge, whose knowledge of scientific terminology is remarkable, especially deserves my thanks in this respect.

Aix galericulata (L.), Mandarin Duck

PROTOZOA

Leucocytozoon sp. (106, 203)
Plasmodium (207)

ARTHROPODA

ACARINA

Freyana anatina dendronessae (136)

TREMATODA

Cotylurus brevis (142, 145*)
Dendritobilharzia pulverulenta (150)
Notocotylus magniovatus (194)

CESTODA

Hymenolepis coronula (37, 241)
Hymenolepis sp. (635)

NEMATODA

Acuaria uncinata (635)
Heterakis sp. (383)
Microfilariae (203)
Syngamus (204)

Aix sponsa (L.), North American Wood Duck

PROTOZOA

Haemoproteus nettionis (163)
sp. (223, 428)
Leucocytozoon (223, 428)

ARTHROPODA

Anaticola crassicornis (231)

MALLOPHAGA

Anaticola lepidotus (231)
Trinoton querquedulae (571)

TREMATODA

Distomum delicatulum (439)
Echinostoma sp. (129)
Notocotylus urbanensis (194, 215, 605)

CESTODA

Diorchis bulbodes (521)
Hymenolepis anceps (521)
Hymenolepis mayhewi (521)
sp. (521, 635)

NEMATODA

Acuaria uncinata (635)
Heterakis caudata (25, 340)
circumvallata (340)
Heterakis dispar (371)
'Gapeworm' not named (114)
Microfilaria (9, 428)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37)

Alopochen aegyptiacus (L.), Egyptian Goose

PROTOZOA

Leucocytozoon simondi (386)

Alopochen aegyptiacus (*cont.*)

ARTHROPODA

MALLOPHAGA

Acidoproctus taschenbergi (231, 460)
Anaticola asymmetricus (231, 460)
Anatoecus icterodes (621)
natatorum (231)
sp. (460)
Colpocephalum africanum (231)
Holomenopon albofasciatum (460)
Lipeurus jejeunus (617)
Trinoton sp. (460)

ACARINA

Alloptes gynurus (460)
Bdellorhynchus psalidurus (460, 486*c*)
Rhinonyssus rhinolethrum (460)

TREMATODA

Trichobilharzia sp. (156)

CESTODA

Fimbriaria fasciolaris (37, 285)
Hymenolepis biaculeata (182, 241, 409)

Amazonetta brasiliensis brasiliensis (Gmelin), Lesser Brazilian Teal

ARTHROPODA

MALLOPHAGA

Anatoecus monteiroi (231)

ACARINA

Freyana furcata (136)

TREMATODA

Amphistoma lunatum (575)
Apatemon globiceps (142)
Echinostoma mendax (129)
Echinostoma revolutum (31, 194, 195)
Typlocoelum obovale (551)
Zygocotyle lunatum (195, 288, 639)

CESTODA

Fimbriaria fasciolaris (178)
Hymenolepis bisaccata (176*c*, 178, 182)
collaris (178, 182)
compressa (37, 241)
megalops (178, 182, 241, 493)
Hymenolepis spp. (635)
Lateriporus biuterina (182)
biuterinus (178, 179)
propeteres (178, 182)
teres (177)

ACANTHOCEPHALA

Corynosoma peposacae (195, 415)
Prosthenorchis avicola (415)

Amazonetta brasiliensis ipecutiri Vieillot, Greater Brazilian or Schuyl's Teal

TREMATODA

Zygocotyle lunatum (194, 288)

Anas acuta acuta L., Northern Pintail (including *Anas acuta tzitzihoa*)

PROTOZOA

Haemoproteus nettionis (163)
sp. (223, 225, 303)
Leucocytozoon sp. (223, 224, 454, 455, 653, 671)
Plasmodium relictum (224)
sp. (224)
Trypanosoma (223, 671)

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solitaria (143, 548)
urbanensis (194, 195, 215)
Ophthalmophagus theodori (195)
Pleurogenoides gastroporus (548)
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ovatus (67)
Psilochasmus oxyurus (67, 548)
Schistogonimus rarus (67)
Sphaeridiotrema globulus (67, 194, 195, 437, 442, 482)
Tracheophilus cymbium (37, 67)
Typhlocoelum cucumerinum (37)
cymbium (194, 195, 378)

CESTODA

Aploparaksis endacantha (138)
furcigera (138)
Diorchis inflata (37)
nyrocae (511, 521)
skrjabini (37)
Fimbriaria fasciolaris (37, 138, 182, 232, 283, 511, 521, 629*b*)
Hymenolepis anatina (182, 195, 241, 283, 351, 494)
bisaccata (137, 138)
collaris (37, 138, 178, 182, 195, 241, 283, 351, 494, 552)
compressa (37, 138, 194, 241)
coronula (37, 138, 521)
dafilae (475)
fausti (138, 521)
gracilis (37, 138)
Hymenolepis mastigopraedita (476)
megalops (37, 138, 178, 182, 195, 241, 283, 351, 493, 494, 521)
octacantha (138, 178, 182, 195, 241, 283, 351, 406, 494)
parvisaccata (543)
simplex (182, 232, 241, 283, 521)
solowiowi (182, 232, 241, 283, 629*b*)
sp. (232, 629*b*)
teresoides (137, 138)
venusta (138)
Microsomacanthus fausti (512)
Sobolevicanthus collaris (511, 512)
octacantha (511)
Weinlandia (Hymenolepis) simplex (629*b*)

Anas acuta acuta (*cont.*)

NEMATODA

Amidostomum anseris (195, 627)
boschadis (511, 512)
Ascaridia galli (195)
perspicillata (195)
Capillaria contorta (118, 369)
Echinuria uncinata (37)
Epomidiostomum uncinatum (26, 195, 382, 627, 655)
Microfilariae (516, 653)
Tetrameres crami (195, 588)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)
Polymorphus cornutus (39)
minutus (37, 195, 351, 415)
sp. (486*b*)

DIOCTOPHYMOIDEA

Eustrongylides mergorum (512)

Anas acuta eatoni (Sharpe), Kerguelen or Eaton's Pintail

CESTODA

Hymenolepis querquedula (182)

Anas americana Gmelin, American Wigeon

PROTOZOA

Haemoproteus nettionis (159)
Leucocytozoon sp. (223, 224)

ARTHROPODA

MALLOPHAGA

Anaticola crassicorne (571)

ACARINA

Freyana largifolia largifolia (136)
Rhinonyssus rhinolethrum (573)

TREMATODA

Amphimerus elongatus (194, 195)
Apatemon gracilis (142)
Cotylurus flabelliformis (194, 195)
Echinostoma revolutum (31, 194, 195)
Pseudobilharziella waubesensis (51)
Zygocotyle lunatum (194, 195)

CESTODA

Diorchis flavescens (521)
Distomum flexum (343)
Epision plicatus (343)
Fimbriariella lintoni (643)
Hymenolepis longivaginata (521)
Hymenolepis megalops (521)
sp. (521)
Taenia compressa (343)
macrocantha (343)

NEMATODA

Amidostomum anseris (255)
Microfilariae (224, 516, 653)
Tetrameres crami (195, 588)

ACANTHOCEPHALA

Corynosoma constrictum (415)
Echinorhynchus striatus (96, 343)

'Anas australis' (? = **Aythya australis australis** (Eyton)), Australian White-eye

CESTODA

Diploposthe laevis (37)

Anas bahamensis bahamensis L., Lesser or Northern Bahama Pintail

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Amphimerus elongatus (195)
Levinseniella cruzi (195, 639)
Maritrema nicolli (195, 639)
Psilochasmus agilis (195, 639)

CESTODA

Hymenolepis flagellata (176*a*, 179, 182, 241)
Hymenolepis lobata (176*a*, 179, 182, 241)

NEMATODA

Acuaria uncinata (635)
Capillaria sp. (369)
Eucoleus raillieti (350)
Strongyloides sp. (511)

ACANTHOCEPHALA

Corynosoma peposacae (195, 415)

Anas bahamensis rubrirostris Vieillot, Greater or Southern Bahama Pintail

TREMATODA

Amphimerus elongatus (194)
Renicola sp. (674, 675)

Anas capensis Gmelin, Cape Teal

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (460)
Anatoecus icterodes (460)

NEMATODA

Acuaria uncinata (635)

Anas castanea (Eyton), Chestnut-breasted Teal

PROTOZOA

Haemoproteus nettii (225)
nettionis (105, 225)
Halteridium nettii (103, 260)
Halteridium nettionis (267)
sp. (262)

CESTODA

Diorchis flavescens (182, 195, 261, 262, 381, 402, 532)
Diploposthe laevis (37, 182, 262)
Fimbriaria fasciolaris (37, 182, 260, 261, 262)
Hymenolepis collaris (182, 261, 262)
megalops (262)

NEMATODA

Acuaria uncinata (635)

Anas clypeata L., Common Shoveler

PROTOZOA

Haemoproteus hermani (224, 225)
Leucocytozoon sp. (203, 224, 225, 455)

Anas clypeata (*cont.*)

ARTHROPODA

MALLOPHAGA

Anaticola crassicorne (151)
crassicornis (43)
Anatoecus dentatus (43)
ferrugineus (231)
Holomenopon setigerum (231)
Laemobothrion laticolle (619)
Lipeurus squalidus (617)
Menopon setigerum (43)
Trinoton querquedulae (43)
squalidum (231)

ACARINA

Bdellorhynchus polymorphus (486*c*)
Freyana largifolia largifolia (136)
Rhinonyssus rhinolethrum (573)
Sternostoma rhinolethrum (692)

TREMATODA

Apatemon gracilis (512)
Bilharziella polonica (37, 511, 512)
Catatropis verrucosa (27, 191, 351, 437)
Cotylurus cornutus (37, 67, 511)
flabelliformis (142, 194, 195, 446)
Echinoparyphium aconiatum (67)
baculus (194, 195)
revolutum (27)
Echinostoma baculus (129, 437)
Echinostomum revolutum (437)
sp. (351)
Hypoderaeum conoideum (37, 129, 194, 195, 288, 351, 437)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 67, 194, 195, 297, 437, 511)
Notocotylus imbricata (195)
Plagiorchis sp. (67)
Prosthogonimus ovatus (53, 56, 130, 194, 195, 288, 351, 437)
Prosthogonimus rarus (54)
Psilochasmus oxyurus (67)
Renicola mediovitellata (66, 67, 675)
Schistogonimus rarus (130, 351, 437)
Tracheophilus cymbium (37, 67)
Trichobilharzia ocellata (511)
Typhlocoelum cucumerinum (37, 67)
cymbium (194, 195)
Typhlophilus shovellus (317)
Zygocotyle lunatum (288)

CESTODA

Anatinella meggitti (512)
Anomotaenia ciliata (37, 138)
Apora dogieli (511)
Diorchis microcirrosa (521)
nyrocae (138, 511)
sp. (512)
Diploposthe laevis (37, 104, 179, 182, 195, 283, 351, 404, 521)
Drepanidotaenia anatina (104)
gracilis (104)
laevis (104)
Echinocotyle clerci (138)
rosseteri (182, 283, 376)
sp. (511)
Fimbriaria fasciolaris (37, 104, 138, 179, 182, 283, 351, 404, 511)
Hymenolepis abortiva (182, 241, 283, 406)
anatina (179, 182, 195, 241, 283, 351, 404)
birmanica (182, 283, 406)
Hymenolepis collaris (37, 182, 241, 283, 406)
echinocotyle (177, 179, 182, 194, 241, 283, 404)
floreata (182, 241, 283)
fragilis (138)
fructicosa (406)
fructifera (182, 241, 283, 406)
fruticosa (182, 406)
gracilis (37, 179, 182, 195, 241, 283, 404)
megalops (37, 138, 182, 241, 283, 681)
neomeggitti (241)
octacantha (108, 138, 179, 182, 195, 241, 283, 351, 404)
pauciannulata (182, 241, 283, 406)
pauciovata (406)
rosseteri (241)
sp. (408)

Anas clypeata (*cont.*)

NEMATODA

Amidostomum boschadis (511)
Capillaria contorta (118, 369)
spinulosa (369)
Eucoleus raillieti (350)
Microfilariae (516)
Porrocaecum crassum (37)
Subulura sp. (397)
Tetrameres crami (195, 588)
Thominx anatis (512)
contorta (511)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)
Polymorphus minutus (37, 38, 39, 195, 415)
sp. (195, 415)

Anas crecca carolinensis (Gmelin), American Green-winged Teal

PROTOZOA

Haemoproteus hermani (224, 225)
nettionis (163)
Leucocytozoon (223, 428)

ARTHROPODA

MALLOPHAGA

Anaticola crassicorne (151)
Trinoton luridum (616)
Trinoton querquedulae (43, 151)

ACARINA

Rhinolyssus rhinolethrum (573)

TREMATODA

Apatemon gracilis (142)
Cotylurus flabelliformis (194, 195)
Echinostoma revolutum (195)
Zygocotyle lunata (478)
lunatum (194, 288)

CESTODA

Aploparaksis furcigera (494)
Cestodes not named (365)
Diorchis acuminata (402, 403, 494, 521, 532)
flavescens (532)
longicirrosa (532)
Diploposthe laevis (494)
Echinocotyle rosseteri (376)
Fimbriaria fasciolaris (494)
Hymenolepis fragilis (494)
gracilis (494)
megalops (37, 494, 521)
octacantha (494)

Anas crecca crecca L., European Green-winged Teal

PROTOZOA

Leucocytozoon simondi (106, 386, 396)

ARTHROPODA

MALLOPHAGA

Anaticola sordidus (231)
Anatoecus icterodes (621)
Trinoton luridum (616)
querquedulae (231)

ACARINA

Bdellorhynchus polymorphus (486*c*)
Freyana anatina (486*c*)
Freyana largifolia largifolia (136)

Anas crecca crecca (*cont.*)

TREMATODA

Apatemon gracilis (511)
Bilharziella polonica (37, 194, 351, 437, 440, 479, 511, 592)
yokogawi (359)
Catatropis verrucosa (437)
Chinhuta indica (318)
Cotylurus cornutus (37, 67, 142, 511)
orientalis (142, 640)
Dendritobilharzia pulverulenta (67)
Distomum marginatum (437)
Echinoparyphium aconiatum (288, 511)
Echinostoma revolutum (67)
sp. (129, 511)
Echinostomum revolutum (437)
Hypoderaeum conoideum (37, 351, 511, 512)
Hypoderaeum gnedini (19, 511)
Notocotylus attenuatus (37, 67, 194, 195, 297, 437, 511, 558)
thienemanni (194, 195, 605)
Plagiorchis laricola (288)
Prosthogonimus cuneatus (130, 194, 195, 558)
ovatus (288)
rarus or intermedius (130)
Pseudobilharziella kowalewskii (150)
Pseudostrigea sarcogyponis (640)
Psilorchis ajgainus (319)
Strigea erratica (437)
tarda (558)
Tracheophilus cymbium (37)

CESTODA

Anatinella meggitti (511)
Anomotaenia ciliata (37, 511)
Aploparaksis furcigera (37, 122, 178, 351, 511)
Dicranotaenia coronula (122)
Diorchis acuminata (104, 122, 178, 182, 195, 261, 283, 532)
Diorchis flavescens (182, 232, 283, 532, 629*a*)
longicirrosa (122, 182, 283, 406, 532)
longiovum (122)
nyrocae (122, 136, 511)
parvogenitalis (37, 122)
(Diorchis) parvogenitalis (393)
Diploposthe laevis (37, 108, 178, 182, 195, 232, 283, 351, 629*a*)
Echinocotyle skrjabini (122)
Fimbriaria fasciolaris (37, 104, 178, 182, 195, 289, 351)
Haploparaxis furcigera (182, 195)
Hymenolepis andrejewa (122)
bisaccata (122)
collaris (37, 182, 241, 283,
coronula (237)
crecca (547)
fasciculata (122)
fausti (122)
Hymenolepis fragilis (178, 182, 195, 232, 283, 351, 629*a*)
gracilis (37, 122, 178, 182, 195, 241, 283, 351)
introversa (182, 232, 283)
krabeella (122, 241)
longicirrosa (241, 410)
megalops (136, 178, 182, 195, 241, 283, 351)
microsoma (241)
octacantha (122, 136, 178, 182, 195, 241, 283, 351)
querquedula (182, 232, 241, 283)
simplex (122, 182, 241, 283)
teresoides (122, 137)
trichorhyncha (195, 241, 283)
trichorhynchus (122, 182)
Lallium magniparuterina (280)
Ligula sp. (104)
Microsomacanthus microsoma (511)
Orlovilepis megalops (122)
Sobolevicanthus collaris (511)
krabeella (511)
Sphenacanthus giranensis (511)
Taenia sp. A (104)

NEMATODA

Amidostomum acuta (627)
acutum (195)
anseris (195, 627)
boschadis (511, 512, 555)
Capillaria anatis (369, 374)
contorta (118, 195, 369, 374)
Echinuria uncinata (37)
Epomidiostomum anatinum (511)
Epomidiostomum orispinum (195, 627)
querquedulae (46, 195, 627)
Eucoleus raillieti (350)
Microfilariae (9)
Tetrameres fissispina (288, 512)
fissispinum (511)
Thominx contorta (511)

Anas crecca crecca (*cont.*)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288)
Polymorphus anatis (195)
Polymorphus magnus (512)
minutus (195, 351, 415)

Anas crecca nimia Friedmann, Aleutian Teal

CESTODA

Diorchis acuminata (524)
longiovum (524)
Fimbriaria fasciolaris (524)
Hymenolepis collaris (524)

Anas cyanoptera cyanoptera Vieillot, Argentine Cinnamon Teal

PROTOZOA

Plasmodium relictum (224)

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Prosthogonimus karausiaki (321)
Prosthogonimus rudolphii (321)

CESTODA

Hymenolepis megalops (322)

NEMATODA

Acuaria uncinata (635)
Epomidiostomum uncinatum (627)

Anas cyanoptera septentrionalium Snyder & Lumsden, Northern Cinnamon Teal

NEMATODA

Epomidiostomum uncinatum (655)

Anas discors discors L., Prairie Blue-winged Teal

PROTOZOA

Haemoproteus nettionis (163)
sp. (607)
Leucocytozoon anatis (222)
sp. (223, 455)

ARTHROPODA

MALLOPHAGA

Anaticola crassicorne (151, 571)
Anataecus (sic) dentatus (151)
Anatoecus dentatus (571)
Trinoton lituratum (151)
querquedulae (151)

ACARINA

Freyana largifolia largifolia (136)

CESTODA

Diorchis kodonodes (529)
microcirrosa (182, 195, 529, 532)
Echinocotyle rosseteri (376)
Hymenolepis filumferens (58, 521)
megalops (37, 322, 521)

Anas discors discors (*cont.*)

NEMATODA

Capillaria anatis (369)
contorta (398)
Tetrameres crami (195, 588)

HIRUDINEA

Theromyzon occidentalis (564)

Anas discors orphna Stewart & Aldrich, Atlantic Blue-winged Teal

CESTODA

Diorchis kodonodes (403)
Diorchis microcirrosa (403)

Anas erythrorhyncha Gmelin, Red-billed Pintail

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (460)
Anatoecus dentatis (sic) (460)
Anatoecus icterodes (460)
Trinoton querquedulae (460)

ACARINA

Rhinonyssus rhinolethrum (460)
Sternostoma rhinolethrum (692)

CESTODA

Diploposthe laevis (17)

TREMATODA

Apatemon gracilis (144)
gracilis minor (142)
Cotylurus flabelliformis (194, 195)
Cyathostoma sp. (79)
Echinoparyphium flexum (426)
Echinostoma revolutum (195)
Eucotyle wehri (194, 195, 480)
Hypoderaeum conoideum (78)
Paramonostomum obtortum (71)
Prosthogonimus karausiaki (130)
Pseudobilharziella querquedulae (50, 194, 195, 363)
Trichobilharzia ocellata (195)
physellae (109)
Zygocotyle lunatum (194, 195)

Anas falcata Georgi, Falcated Teal

PROTOZOA

Haemoproteus sp. (107)
'Leucocytozoa' (474)
Leucocytozoon sp. (106)
Plasmodium praecox (474)

ARTHROPODA

MALLOPHAGA

Trinoton gracile (231)

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Pachytrema calculus (680)

Anas ferina

CESTODA

Diploposthe laevis (37)

Anas formosa Georgi, Baikal or Formosa Teal

ARTHROPODA

MALLOPHAGA

Trinoton gracile (231)

TREMATODA

Apatemon gracilis minor (142)

Apatemon minor (194, 195, 676)

CESTODA

Anomotaenia sp. (232)

Fimbriaria fasciolaris (37)

Hymenolepis simplex (182, 232)

Weinlandia (Hymenolepis) simplex (629*b*)

NEMATODA

Microfilariae (534)

Anas georgica spinicauda Vieillot, Chilean Pintail

TREMATODA

Psilochasmus oxyurus (604)

Anas gibberifrons gibberifrons S. Müller, East Indian Grey Teal

ARTHROPODA

MALLOPHAGA

Anaticola major (231)

Lipeurus anatis major (269)

Lipeurus squalidus var. major (617)

CESTODA

Diorchis flavescens (529)

Hymenolepis robertsi (241)

Anas gibberifrons gracilis Buller, Australian Grey Teal

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Trichobilharzia sp. (28)

CESTODA

Aploparaksis veitchi (24)

Diorchis flavescens (24)

Hymenolepis robertsi (24)

NEMATODA

Echinuria querquedulae (278)

Anas leucophrys Vieillot, Ringed Teal

ARTHROPODA

ACARINA

Freyana leucophrysi (136)

Anas penelope L., European Wigeon

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (43)
penelopes (sic) (231)
Anatoecus dentatus (43)
icterodes (621)
Docophorus icteroides (231, 619)
Holomenopon marecae (231)
Lipeurus jejeunus (617)
Trinoton spinosum (231, 616)

TREMATODA

Apatemon gracilis (142)
Catatropis verrucosa (351, 437)
Cotylurus cornutus (37)
syrius (67, 139, 142)
Echinoparyphium nordiana (37)
Echinostoma paraulum (129, 437)
revolutum (37, 67, 129, 194, 195, 437)
Echinostomum paraulum (351)
Echinostomum revolutum (351)
Hindia lucknowensis (316)
Notocotylus attenuatus (27, 37, 194, 195, 437, 511, 679)
indicus (315)
Opisthorchis simulans (18, 191, 194, 195, 437)
Paramonostomum alveatum (351)
Psilochasmus oxyurus (67)

CESTODA

Dicranotaenia coronula (393)
Diorchis acuminata (104, 178, 182, 195, 261, 283, 351, 402, 403, 494, 529, 532)
Drepanidotaenia acuminata (104)
fasciata (104)
sinuosa (104)
Fimbriaria fasciolaris (37, 178, 182, 195, 283, 351, 494)
Hymenolepis collaris (37, 178, 182, 195, 283, 351, 494, 552)
compressa (37, 195, 241)
Hymenolepis coronula (37)
fallax (178, 182, 195, 241, 351, 494)
fasciata (178, 351)
fasciculata (182, 195, 241, 283, 494)
gracilis (37, 178, 182, 195, 241, 283, 351, 494)
megalops (37, 138)
microsoma (195, 241)
Monopylidium infundibulum (562)

NEMATODA

Amidostomum anseris (195, 555, 627)
Capillaria spinulosa (369)
Echinuria (Acuaria) uncinata (37)
uncinatum (195)
Epomidiostomum orispinum (195, 627)
uncinatum (27, 195, 627, 655)
Trichostrongylus tenuis (374)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)
minutus (195, 351, 415)

Anas platalea Vieillot, Argentine Red Shoveler

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

CESTODA

Hymenolepis megalops (37)

Anas platyrhynchos fulvigula Ridgway, Florida Duck (including *Anas obscura*)

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Cotylurus flabelliformis (142)

CESTODA

Diploposthe laevis (37, 178, 182)
Drepanidotaenia lanceolata (182)
Hymenolepis lanceolata (178)
Hymenolepis macrostrobiloides (sic) (182)
Raillietina (R.) penelopina (288)

NEMATODA

Avioserpens denticulophasma (646)

Anas platyrhynchos platyrhynchos L., Mallard (not including the domestic duck) (q.v.)

PROTOZOA

Eimeria anatis (462)
truncata (301)
Haemoproteus hermani (224, 225)
nettionis (89, 163, 223, 653, 671)
Haemoproteus sp. (225)
Leucocytozoon simondi (84, 85, 86, 88, 386)
sp. (106)
Plasmodium lophurae (240)
Tyzzeria perniciosa (6)

ARTHROPODA

MALLOPHAGA

Anaticola crassicorne (151)
crassicornis (43, 231)
Anatoecus dentatus (43, 231)
Lipeurus squalidus (619)
Menopon setigerum (43)
Trinoton querquedulae (43, 151)

SIPHONAPTERA

Ceratophyllus garei (509)

ACARINA

Rhinonyssus rhinolethrum (573)

HIRUDINEA

Dina parva (486*b*)
Placobdella rugosa (486*b*)
Protoclepsis tesselata (505)
Theromyzon sp. (486*b*)

TREMATODA

Amphimerus anatis (67, 194, 195)
elongatus (194, 195)
filiformis (244)
fuligulae (195)
Apatemon gracilis (142, 194, 195, 446, 511, 512)
gracilis fuligulae (142)
gracilis japonicus (142)
gracilis minor (142)
gracilis pellucidus (142)
japonicus (243, 244)
Apatemon minor (194, 195, 676, 680)
parvitestis (142, 244)
Bilharziella polonica (67, 194, 195, 351, 437, 479, 511, 557, 591)
yokogawai (49)
Catatropis verrucosa (194, 195, 437)
Cotylurus brevis (142)
cornutus (37, 67, 142, 194, 195, 512, 594)
flabelliformis (194, 195)
Cotylurus hebraicus (67)

Anas platyrhynchos platyrhynchos (*cont.*)

TREMATODA (*cont.*)

Cyathocotyle fusa (142)
orientalis (142)
prussica (67, 142)
sp. (511)
szidatiana (142)
Cyathocotyloides curonensis (601)
Cyclocoelum pseudomicrostomum (194)
Dendritobilharzia anatinarum (82)
pulverulenta (49, 67, 194, 195)
Dicrocoelium sp. (351, 437)
Echinochasmus beleocephalus chankensis (135)
Echinoparyphium cinctum (511)
clerci (67)
koidzumii (243, 244)
nordiana (37)
recurvatum (37, 67, 195, 456)
Echinostomum elongatum (194)
minor (194)
miyagawai (243, 244)
paraulum (351, 437)
revolutum (37, 67, 194, 195, 244, 351, 437, 549)
Gigantobilharzia monocotylea (194, 195, 596)
Hypoderaeum conoideum (27, 37, 67, 194, 195, 288, 351, 437, 456, 511, 512, 549)
sinensis (194)
Levinseniella pellucida (194, 195, 351, 437)
Metorchis coeruleus (219)
orientalis (244, 288)
pinguincola (219)
tener (219)
xanthosomus (194, 195, 219, 557)
Monostomum minutissimum (297, 437)
Neodiplostomum sp. (67)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 67, 194, 195, 243, 244, 437, 511, 512, 676, 679)
seineti (194, 195, 605)
skrjabini (1)
Notocotylus thienemanni (194, 195, 605)
urbanensis (194, 195)
Ophthalmophagus massinowi (194)
Opisthorchis anatis (676)
geminus (194, 195, 437)
simulans (194, 195, 437, 512)
Orchipedum tracheicola (37)
Paramonostomum ovatus (194, 195)
Parastrigea anati (67)
robusta (142, 594)
Plagiorchis potanini (194, 195)
sp. (67, 558)
Prosthogonimus cuneatus (558)
japonicus (130, 194, 195, 243, 244)
macrorchis (130, 194, 195)
orientalis (130, 194, 676, 680)
ovatus (130, 194, 288)
pellucidus (130)
rarus (53, 56)
rudolphii (130, 194, 195)
skrjabini (130)
sp. (557)
sp. plur. (130)
Psilochasmus japonicus (244)
lecithosus (195)
longicirratus (233, 234)
oxyurus (67)
Schistogonimus rarus (67, 130, 194, 195, 437)
varies (sic) (557)
Tetracotyle ardeae (512)
sp. (351)
Tracheophilus cymbium (37)
sisowi (511, 549, 551, 557, 591, 662)
Trematoda not named (365)
Trichobilharzia ocellata (109, 364, 511, 512)
physellae (109, 364)
Tylodelphys excavata (37)
Typhlocoelum cucumerinum (37, 194, 195)
cymbium (30, 67, 194, 195)
Uniserialis gippyensis (36)
Zygocotyle ceratosa (97, 437, 574)
lunatum (195, 486*b*, 659)

CESTODA

Anomotaenia ciliata (37, 138, 182, 283, 511, 512)
Aploparaksis acicula-sinuata (532)
furcigera (37, 122, 137, 138, 178, 351, 494, 511)
japonensis (122)
pseudofurcigera (393)
rhomboidea (339)
stefańskii (121)
Cestoda not named (365)
Cotugnia fasciata (195)
Davainea anatina (180)
Dicranotaenia collaris (137)
coronula (121, 137, 511, 512)
coronula subsp. micracantha (393)
fausti (137)
Diorchis bulbodes (121, 195, 283, 521, 532, 641)

Anas platyrhynchos platyrhynchos (*cont.*)

CESTODA (*cont.*)

Diorchis flavescens (511)
formosensis (532, 583)
inflata (37)
nyrocae (121, 511, 512)
parvogenitalis (37, 121, 137, 512)
ransomi (37)
skrjabini (37, 137)
spinata (511)
stefańskii (121)
Diploposthe laevis (37, 178, 182, 195, 283, 351, 629*b*)
Drepanidotaenia octacantha (104)
sinuosa (104)
Fimbriaria fasciolaris (37, 104, 137, 138, 178, 182, 195, 283, 351, 456, 494, 511, 521, 529*b*, 554, 557)
fausti (511)
plana (178, 182, 195, 283, 339, 351, 494)
sp. (486*b*)
Fuhrmanniella fausti (629*b*)
Haploparaksis furcigera (195)
japonensis (121, 195, 678)
Hymenolepis abortina (339)
abortiva (121, 178, 182, 195, 241, 283, 351, 406)
acicula (37, 195)
acicula-sinuata (182, 241, 283, 508)
aequabilis (121)
anatina (121, 178, 182, 195, 241, 283, 351, 494)
angularostris (241)
collaris (27, 37, 138, 178, 182, 195, 241, 283, 351, 486*b*, 494, 552, 557)
compressa (37, 121, 137, 138, 195, 241, 557)
coronula (37, 138, 178, 182, 195, 241, 283, 339, 351, 456, 494, 554, 557)
echinocotyle (121, 182, 232, 241, 283, 521)
fausti (121, 182, 232, 241, 283, 521)
furcigera (178, 182, 283)
giranensis (241)
gracilis (37, 138, 178, 182, 195, 241, 283, 351, 456, 494, 521)
(Sobolevicanthus) gracilis (121)
introversa (195, 241, 402, 521)
jägerskioldi (121, 182, 241, 283)
jamunica (121)
lanceolata (195, 241)
macrocephala (37, 182, 241, 283)
Hymenolepis macrostrobilodes (sic) (521)
megalops (37, 138, 195, 232, 241, 493, 521, 554)
microsoma (108)
nyrocae (121, 241, 521, 678)
octacantha (138, 178, 182, 195, 241, 283, 351, 494)
oshimai (241)
paracompressa (121)
paramicrosoma (121, 138, 241, 283)
parvula (121, 182, 195, 241, 281, 283, 302)
pittalugai (349)
rosseteri (195, 241)
sacciperium (121)
sagitta (195, 241)
setigera (121, 182, 241, 283)
sp. (108, 266, 408, 456)
'sp. Skrjabin' (121)
spiralbursata (121)
tenuirostris (195)
teresoides (121, 138)
trifolium (121, 178, 182, 195, 241, 283, 339, 351, 494)
tritesticulata (121, 182, 232, 241, 283)
venusta (138, 241, 641)
(Sobolevicanthus) krabbeella (121)
octacantha (121)
Ligula intestinalis (37, 195, 283, 351)
Microsomacanthus compressa (511)
fausti (512)
microsoma (511)
parvula (511)
Orlovilepis infrequens (121)
megalops (121, 511)
Raillietina anatina (195)
microcotyle (195)
parviuncinata (195, 232, 629*b*)
Schistocephalus solidus (37, 72, 283)
Sobolevicanthus collaris (511, 512)
gracilis (511, 512)
krabeella (511, 512)
octacantha (511, 512)
Sphenacanthus giranensis (511)
Taenia anatina (508)
conica (178, 494)
sinuosa (347)
Tschertkovilepis setigera (511)
Weinlandia (Hymenolepis) megalops (629*b*)
tritesticulata (629*b*)

Anas platyrhynchos platyrhynchos (*cont.*)

NEMATODA

Agamospirura sp. (555)
Amidostomum anseris (557, 627)
boschadis (511, 512)
skrjabini (627)
Ascaridia galli (195)
lineata (623)
Ascaridia staphlocerca (195)
Capillaria anatis (369, 374, 456, 557)
contorta (118, 195, 369, 374)
spinulosa (369)
sp. (37)
Contracaecum microcephalus (195)
Diplotriaena microphallos (333)
Echinuria jagadornata (195)
jugodornata (55)
uncinata (37, 400)
uncinatum (557)
Epomidiostomum anatinum (511, 512, 555)
orispinum (627)
uncinatum (30, 195, 627, 655)
Eucoleus raillieti (350)
Filaria anatis (333)
'Gapeworm' (114)
Heterakis dispar (195)
lineata (337)
vesicularis (337, 555, 623)
Microfilariae (87, 89, 224, 516, 653)
Porrocaecum crassum (37, 195, 511)
ensicaudatum (195)
Streptocara crassicauda (195, 486*b*, 555)
Syngamus trachea (195, 656)
Tetrameres americana (116)
crami (195, 587)
fissispina (288, 456, 512, 624)
fissispinus (195, 511, 557)
inflata (624)
paradoxa (624)
Thominx anatis (511, 512)
contorta (511, 512)
Trichostrongylus tenuis (120, 195, 374)

ACANTHOCEPHALA

Acanthocephala not named (365)
Acanthocephalus ranae (37)
Echinorhynchus filicollis (391)
laevis (339)
longicollis (391)
mergorum (512)
polymorphus (390)
sphaerocephalus (391)
Filicollis anatis (37, 288, 351, 415)
Polymorphus 'acutis' (101)
anatis (195)
botulus (195)
corynoides (195, 415)
magnus (511, 512)
matthevosianae (sic) (468)
minutus (37, 38, 195, 445, 557)
Profilicollis botulus (30)

DIOCTOPHYMOIDEA

Eustrongylides elegans (555)
Hystrichis tricolor (195, 217, 289, 511)

Anas poecilorhyncha poecilorhyncha Forster, Indian Spotbill (including '*Anas poecilorhyncha*')

PROTOZOA

Plasmodium sp. (312)

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Echinostoma revolutum (190)
Paryphostomum horai (20)

Anas poecilorhyncha poecilorhyncha (*cont.*)

CESTODA

Aploparaksis sp. (410)
Fimbriaria fasciolaris (410)
Hymenolepis collaris (37, 241, 410)
coronula (37)
Hymenolepis foveata (241, 410)
introversa (241, 410)
sp. (? collaris) (566)

Anas poecilorhyncha zonorhyncha Swinhoe, Chinese Spotbill

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Notocotylus attenuatus (679)
Psilochasmus longicirratus (680)

Anas punctata Burchell, Hottentot Teal

ARTHROPODA

MALLOPHAGA

Lipeurus squalidus (618)

ACARINA

Freyana largifolia (460)

CESTODA

Taenia flavescens (305)

Anas querquedula L., Garganey

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (43)
Anatoecus dentatus (43)
Menopon setigerum (43)
Trinoton luridum (616)

ACARINA

Freyana anatina (486*c*)

TREMATODA

Apatemon gracilis (142)
gracilis var. exilis (141)
Bilharziella polonica (37, 67, 150, 194, 195, 437, 470, 511)
pulverulenta (55, 56, 437, 441)
Catatropis verrucosa (351, 437)
Cotylurus cornutus (37, 67, 511)
Cyathocotyle prussica (141, 142)
sp. (511)
Dendritobilharzia pulverulenta (150, 194, 479)
Echinoparyphium aconiatum (67)
clerci (67)
recurvatum (37, 511)
Echinostoma chasma (320)
revolutum (37, 129)
Echinostomum revolutum (351, 437, 511)
Hypoderaeum conoideum (37, 129, 194, 195, 351, 437)
Metorchis crassiusculus (194, 195)
xanthosomus (56, 194, 195)
xanthosomus var. compascuus (437)

Anas querquedula (*cont.*)

TREMATODA (*cont.*)

Notocotyle triserialis (351)
Notocotylus attenuatus (37, 67, 194, 195, 437, 511)
seineti (194, 195, 437)
Prosthogonimus querquedulae (130, 194, 195, 676)
Psilochasmus oxyurus (67)
Schistogonimus rarus (67, 511)
Strigea sp. (37)
Trichobilharzia kossarewi (479)
ocellata (511)

CESTODA

Anatinella meggitti (511)
Aploparaksis furcigera (511)
Diorchis acuminata (137)
kodonoides (sic) (195)
microcirrosa (195)
nyrocae (122, 138, 511)
parvogenitalis (37, 122)
skrjabini (37)
Dicranotaenia coronula (122)
fausti (138)
Diploposthe laevis (37, 179, 182, 195, 283)
Echinocotyle clerci (122, 138)
minutissima (547)
rosseteri (122, 511)
Fimbriaria fasciolaris (37, 138, 178, 182, 194, 283)
Hymenolepis collaris (37)
coronula (37)
fallax (122, 179, 182, 241, 283)
gracilis (37)
krabeella (122, 195)
megalops (37)
nyrocae (122)
octacantha (122, 138)
paracompressa (122)
spiralbursata (122)
tenuirostris (122)
Microsomacanthus parvula (511)
Orlovilepis megalops (122, 511)
Sobolevicanthus collaris (511)

NEMATODA

Acuaria uncinata (635)
Amidostomum anseris (195, 627)
boschadis (511)
Capillaria anatis (194, 350, 369, 625)
contorta (369, 374)
spinulosa (369)
Echinuria uncinata (37)
Epomidiostomum anatinum (511)
uncinata (384)
uncinatum (26, 627)
Eucoleus raillieti (350)
Terameres fissispinum (511)
Thominx contorta (511)

ACANTHOCEPHALA

Filicollis anatis (37)
Polymorphus boschadis (27)
Polymorphus cornutus (39)
minutus (37, 38)

DIOCTOPHYMOIDEA

Hystrichis neglectus (195)

Anas rhynchotis rhynchotis Latham, Australian Shoveler

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Echinostoma revolutum (264)

CESTODA

Diorchis flavescens (182, 195, 260, 261, 381, 402, 529, 532)
Taenia flavescens (178)

Anas rubripes Brewster, North American Black Duck (including *Anas fulvigula rubripes*)

PROTOZOA

Haemoproteus anatis (200, 201, 222, 227)
hermani (227)
nettionis (163)
sp. (220, 221)
spp. ? (227)
Leucocytozoon (95, 159, 428, 454, 455)
spp. (227)
'Plasmodiidae' (227)
Tyzzeria sp. (164)

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Amphimerus elongatus (194, 195)
Apatemon gracilis (142)
Cotylurus flabelliformis (142, 194, 195, 446)
Echinstoma revolutum (194, 195)
Leucochloridiomorpha macrocotyle (194, 195)
Maritrema acadiae (194, 195, 491)
Prosthogonimus anatinus (130, 194, 195)
Prosthogonimus macrorchis (195)
rudolphii (130, 194, 195)
A schistosome not named (49)
Streptovitella acadiae (585)
Typhlocoelum cucumerinum (194, 195)
cymbium (194, 195)
Zygocotyle lunatum (194, 195)

CESTODA

Diorchis flavescens (521)
Diplopostheae laevis (37, 494)
Fimbriaria fasciolaris (37, 521, 643)
Haploparaksis japonicus (521)
Hymenolepis collaris (521)
compressa (37, 521)
coronula (37)
Hymenolepis fausti (520, 521)
gracilis (37, 521)
hopkinsi (520, 521)
introversa (241)
lanceolata (241, 494)
macrostrobilodes (sic)(241, 521)
megalops (37, 521)

NEMATODA

Capillaria anatinis (398)
spp. (398)
Contracaecum anasi (397)
Echinuria uncinata (37, 114, 194)
'Gapeworm' not named (114)
Microfilaria (9, 95, 428)
Ornithofilaria fallisensis (10, 11)
Tetrameres crami (194, 588)

Anas sibilatrix Poeppig, Chiloe Wigeon

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

CESTODA

Hymenolepis megalops (37)

NEMATODA

Acuaria uncinata (635)
Amidostomum skrjabini (23, 627)

Anas sp.

PROTOZOA

'Coccidium' (311)
Haemoproteus sp. (105, 533)

Anas sp. (*cont.*)

ARTHROPODA

MALLOPHAGA

Lipeurus squalidus (617)

ACARINA

Freyana anatina anatina (136)

TREMATODA

Distomum choledocum (337)
Echinostomum sp. (558)
Prosthogonimus sp. (130)
Psilostomum oxyurus (56)

CESTODA

Aploparaksis rhomboidea (339)
Cittotaenia avicola (173, 182)
Cotugnia fastigata (13, 182)
Davainea cyrtus (553)
Diorchis anomala (529)
flavescens (182, 232, 529)
Diploposthe laevis (554)
Fimbriaria fasciolaris (232, 554)
plana (339)
Hymenolepis abortina (339)
coronula (339)
megalops (97, 554)
meggitti (182, 232, 629*b*)
simplex (182, 232)
trifolium (339)
Raillietina (R.) cyrtus (182)
penelopina (288)
Weinlandia (Hymenolepis) simplex (629*b*)

NEMATODA

Ascaris ensicaudata (339)

ACANTHOCEPHALA

Echinorhynchus anatis (391)
laevis (339)
Filicollis anatis (568)
Polymorphus minutus (415, 568)

Anas sparsa leucostigma Rüppell, Abyssinian Black Duck

CESTODA

Hymenolepis spp. (635)

NEMATODA

Acuaria uncinata (635)

Anas sparsa sparsa Eyton, African Black Duck

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)
Rhinonyssus rhinolethrum (460)

NEMATODA

Acuaria uncinata (635)

Anas strepera strepera L., Gadwall

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (43)
depuratus (231)
Anatoecus dentatus (43)
Trinoton querquedulae (43)

Anas strepera strepera (*cont.*)

ARTHROPODA (*cont.*)

ACARINA

Freyana largifolia largifolia (136)
Rhinonyssus rhinolethrum (573)

TREMATODA

Cotylurus cornutus (37, 67)
Echinoparyphium recurvatum (37, 67)
revolutum (37, 67)
Echinostoma sp. (129)
Echinostomum sp. (351, 437)
Hypoderaeum conoideum (37, 67)
Notocotylus attenuatus (37, 67)
Prosthogonimus ovatus (130)
Psilochasmus oxyurus (67)
Psilotrema simillimum (67)
Renicola mediovitellata (66, 67, 675)
Strigea sp. (437)
Tracheophilus cymbium (37, 67)
Trichobilharzia ocellata (512)
Typhlocoelum americanum (486*b*)
cucumerinum (37)

CESTODA

Aploparaksis furcigera (37, 122, 138)
Apora dogieli gynezinskaya (138)
Diorchis acuminata (122, 178, 182, 261, 283, 351, 402, 403, 494, 529)
spinata (122, 182, 283, 403, 529)
stefańskii (122)
tshanensis (122, 138)
Diploposthe laevis (37, 104, 178, 182, 283, 494)
Drepanidotaenia anatina (104)
fragilis (104)
gracilis (104)
octacantha (104)
Echincotyle skrjabini (122)
Eucotyle zakharowi (67)
Fimbriaria fasciolaris (37, 138)
Hymenolepis anatina (122, 178, 182, 195, 241, 283, 351, 494)
bisaccata (137, 138)
collaris (37)
compressa (37, 122, 138)
fragilis (178, 182, 195, 283, 351, 494)
gracilis (37, 138, 178, 182, 195, 241, 283, 351, 494)
krabeella (241)
megalops (138)
octacantha (178, 182, 195, 283, 351, 494)
teresoides (122, 137, 138, 178, 182, 195, 241, 283, 351, 494)
Ligula sp. (104)
Orlovilepis megalops (122)

NEMATODA

Acuaria uncinata (635)
Amidostomum boschadis (512)
skrjabini (23, 27, 627)
Capillaria contorta (118, 369)
Echinuria uncinata (37)
Epomidiostomum uncinatum (512)
Porrocaecum crassum (37)
Tetrameres crami (195, 588)
fissispina (288)

ACANTHOCEPHALA

Polymorphus cornutus (39)
mathevosianae (467)
Polymorphus minutus (37, 195, 415)

Anas superciliosa pelewensis Hartlaub & Finsch, Pelew Island Grey Duck

CESTODA

Diorchis flavescens (532)

Anas superciliosa rogersi Mathews, Australian Black Duck

TREMATODA

Echinostoma revolutum (258, 259, 263, 264, 436)
Echinostoma sp. (262)
Notocotylus attenuatus (258, 263, 436)

Anas superciliosa rogersi (*cont.*)

CESTODA

Diorchis flavescens (182, 260, 261, 262, 381)
Diploposthe laevis (182, 262)
Fimbriaria fasciolaris (178, 182, 260, 261, 262)
Hymenolepis collaris (182, 260, 261, 262)
megalops (182, 260, 261, 262)
Taenia bairdi (178, 305, 589)
cylindrica (178 305)
flavescens (178, 305)
pediformis (178, 305)

NEMATODA

Physaloptera sp. (273)
Tetrameres fissispina (277)

Anas superciliosa superciliosa Gmelin, New Zealand Grey Duck

ARTHROPODA

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Echinostoma revolutum (31, 194, 195)
Nocotylus attenuatus (195)

CESTODA

Diorchis acuminata (402)
flavescens (195, 529)
Diploposthe laevis (37)
Fimbriaria fasciolaris (37)

Anas undulata undulata Du Bois, African Yellowbill

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (460)
Anatoecus icterodes (460)
Trinoton querquedulae (460)

ACARINA

Freyana largifolia largifolia (136)

TREMATODA

Trichobilharzia sp. (156)

NEMATODA

Acuaria uncinata (635)

Anatidae spp.

ARTHROPODA

ACARINA

Leptospira velata (486*c*)

TREMATODA

Cyclocoelum neivai (282)
Tracheophilus neivai (662)
Typhlocoelum neivai (639)

CESTODA

Diphyllobothrium ditremum (388)

'Anatine Birds'

CESTODA

Taenia sensu lato (286)

NEMATODA

Capillaria anatis (373)
Capillaria contorta (373)

Anser albifrons albifrons (Scopoli), European White-fronted Goose

PROTOZOA

Leucocytozoon (223)

ARTHROPODA

MALLOPHAGA

Anaticola serratus (231)
Anatoecus brevimaculatus (231)
Anatoecus icterodes (621)
Trinoton squalidum (231)

TREMATODA

Apatemon gracilis (195, 594)
Catatropis verrucosa (437)
Hypoderaeum conoideum (37, 129, 437)
Notocotylus attenuatus (297, 437)
Notocotylus magniovatus (679)
parviovatus (679)
Strigea gracilis (?) (437)

CESTODA

Hymenolepis barrowensis (522)
creplini (241, 283, 494, 522)
fasciata (178)
Hymenolepis fasciculata (182, 283, 494)
setigera (241)

NEMATODA

Amidostomum anseris (195, 594, 627)
skrjabini (23, 25, 46, 627)
spatulatum (27)
Epomidiostomum orispinum (27, 195, 627)
Epomidiostomum skrjabini (627)
uncinatum (195, 627)
Trichostrongylus tenuis (27, 120, 195, 374)

Anser albifrons frontalis Baird, Pacific White-fronted Goose

PROTOZOA

Eimeria farri (211)
magnalabia (211)
Leucocytozoon (671)
Tyzzeria anseris (211)

TREMATODA

Catatropis verrucosa (351)
Hypoderaeum conoideum (351)
Notocotyle triserialis (351)

CESTODA

Hymenolepis creplini (351)
Hymenolepis fasciata (351)

NEMATODA

Epomidiostomum uncinatum (655)
Microfilariae (516)

Anser anser anser (L.), Western Greylag Goose (excluding the domestic goose) (q.v.)

PROTOZOA

Eimeria anseris (213)
nocens (213)
parvula (213)
Eimeria truncata (93, 213, 301, 658)
Leucocytozoon anseris (106)
sp. (172, 251*a*, 658)

Anser anser anser (*cont.*)

ARTHROPODA

MALLOPHAGA

Anaticola anseris (43, 231)
Anatoecus dentatus (43)
Cicinophilus parvus (231)
Colpocephalum pectiniventre var. parvum (43)
Trinoton anserinus (43, 231)
continuum (616)

ACARINA

Freyana anserina (486*c*)
Sternostoma rhinolethrum (692)

TREMATODA

Catatropis verrucosa (351, 437, 549)
Cercarioides baylisi (191)
Cotylurus cornutus (37)
Cyclocoelum arcuatum (282)
Echinostoma revolutum (31, 37)
sp. (129)
Echinostomum revolutum (437)
Hypoderaeum conoideum (129, 351, 437)
Hyptiasmus tumidus (297, 437, 662)
Monostomum arcuatum (437)
mutabile (?) (437)
Notocotylus attenuatus (37, 67, 437)
Paramonostomum alveatum (195, 297, 351, 437)
Prohyptiasmus robustus (67)
Prosthogonimus cuneatus (130, 288)
horiuchii (130)
japonicus (130)
ovatus (67, 130, 288)
pellucidus (130)
sp. (130)
Schistogonimus rarus (63)

CESTODA

Aploparaksis furcigera (37, 122)
Dicranotaenia coronula (104, 122)
Diorchis stefańskii (122)
Diploposthe laevis (37)
Drepanidotaenia bilateralis (138)
coronula (104, 122)
lanceolata (104, 122, 138)
przewalskii (122)
setigera (104)
Fimbriaria fasciolaris (37, 138, 195)
Hymenolepis anatina (195, 241)
collaris (37, 178, 182, 195, 241, 283, 351, 494, 552)
compressa (37, 241)
conscripta (241)
Hymenolepis coronula (37, 178, 182, 195, 241, 283, 351, 494)
creplini (138, 178, 182, 241, 283, 351, 494, 554)
fasciata (178, 351)
fasciculata (122, 138, 182, 195, 241, 283, 494)
gracilis (122, 195, 241)
lanceolata (195, 241, 260, 494, 554)
longicirrosa (554)
paracompressa (122)
przewalskii (182, 241, 283, 554)
setigera (122, 138, 178, 182, 195, 241, 283, 351, 494, 554)
tenuirostris (122, 195, 241)

NEMATODA

Amidostomum anseris (195, 350, 456, 555, 627)
Capillaria anatis (195, 456, 625)
anseris (456)
caudinflata (456)
Echinuria uncinata (37)
Epomidiostomum orispinum (195, 627)
Eucoleus raillieti (350)
Heterakis dispar (104)
gallinae (456)
Microfilariae (658)
Syngamus trachea (195)
Tetrameres paradoxa (624)
Trichostrongylus tenuis (120, 195, 196, 374, 456)

ACANTHOCEPHALA

Filicollis anatis (37, 288)
Polymorphus anatis (37, 195)

DIOCTOPHYMOIDEA

Eustrongylides papillosus (195)

Anser brachyrhynchus Baillon, Pink-footed Goose

ARTHROPODA

SIPHONAPTERA

Ceratophyllus vagabunda insularis (509)

TREMATODA

Catatropis verrucosa (27)

CESTODA

Hymenolepis creplini (27)
Hymenolepis megalops (252)

NEMATODA

Amidostomum anseris (252)
nodulosum (27)
Amidostomum spatulatum (27)
Trichostrongylus tenuis (27, 252, 374)

Anser canagicus Sewastianow, Emperor Goose

CESTODA

Hymenolepis barrowensis (524)
lanceolata (524)
Hymenolepis philactis (519)

Anser coerulescens atlanticus Kennard, Greater Snow Goose

PROTOZOA

Eimeria truncata (635)
Tyzzeria anseris (211)
Tyzzeria sp. (64)

CESTODA

Drepanidotaenia lanceolata (376)

NEMATODA

Amidostomum spatulatum (399)
Trichostrongylus tenuis (399)

Anser coerulescens coerulescens (L.), Lesser Snow Goose and Blue Goose (including *A. coerulescens hyperboreus* and *Chen coerulescens hyperboreus*)

PROTOZOA

Coccidian oocysts (327)
Eimeria anseris (211)
clarkei (211)
fulva (211)
hermani (211)
magnalabia (211)
Eimeria nocens (211)
truncata (211)
Oocysts, possibly of Eimeria parvula and Tyzzeria sp. (326)
Tyzzeria anseris (211)

ARTHROPODA

ACARINA

Freyana anserina (486*c*)

TREMATODA

Cyathostoma brantae (73)
Notocotylus attenuatus (73)

CESTODA

Cestode eggs not identified (326)

Anser coerulescens coerulescens (*cont.*)

NEMATODA

Amidostomum sp. (119)
Epomidiostomum crami (627, 655)
sp. (119)
Heterakis dispar (371)
Heterakis hyperborea (590)
Strongylid eggs, not identified (326)
Trichostrongylus tenuis (119, 120, 371, 399)

Anser cygnoides (L.), Swan Goose

ARTHROPODA

MALLOPHAGA

Anaticola cygnopsis (231)
Anatoecus brunniceps (231)
Ornithobius mathisi (231)

TREMATODA

Prosthogonimus horiuchii (420)

CESTODA

Diploposthe laevis (37, 178, 182)
Hymenolepis longicirrosa (176*a*, 178, 182, 241)

Anser erythropus (L.), Lesser White-fronted Goose

TREMATODA

Cotylurus cornutus (37)

Anser fabalis fabalis (Latham), Western or Yellow-billed Bean Goose

TREMATODA

Catatropis verrucosa (351, 437)
Echinoparyphium revolutum (27)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 297, 437)

CESTODA

Hymenolepis pingi (241)
pingis (283)
longicirrosa (241, 283)
Hymenolepis longistylosa (241, 283)
setigera (178, 182, 283, 351, 494)

NEMATODA

Amidostomum spatulatum (23, 27)
Epomidiostomum orispinum (27)
Heterakis dispar (371)

Anser fabalis serriorostris Swinhoe, Thick-billed or Eastern Bean Goose

ARTHROPODA

MALLOPHAGA

Nirmus argulus (620)

TREMATODA

Echinostoma anseris (680)
Notocotylus attenuatus (297)
Notocotylus magniovatus (679)
orientialis (308)

CESTODA

Hymenolepis pingi (232)
longicirrosa (232, 629*b*)
Hymenolepis longistylosa (232, 629*b*)
Taenia setigera (347)

Anser fabalis serriorostris (*cont.*)

NEMATODA

Amidostomum anseris (555, 627)
spatulatum (627)
Epomidiostomum orispinum (627)

Anser indicus Latham, Bar-headed Goose

PROTOZOA

Eimeria truncata (635)

Anser rossii Cassin, Ross's Goose

PROTOZOA

Eimeria truncata (211)

NEMATODA

Amidostomum sp. (449)

Anser sp.

PROTOZOA

Coccidium truncatum (311)

TREMATODA

Holostephanus lutzi (142)

CESTODA

Diorchis bulbodes (170)
laevis (170)
Hymenolepis linea (241)
meggitti (241)

Anser sylvestris (= **Anser anser anser** (L.), Western Greylag Goose)

Hymenolepis longicirrosa (182)
longistylosa (182)
Hymenolepis pingi (182)

Anseranas semipalmata (Latham), Magpie Goose

ARTHROPODA

MALLOPHAGA

Acidoproctus hilli (231)

ACARINA

Fryanopsis decidilatatusetae (136)

TREMATODA

Cyclocoelum obscurum (282)
Echinostoma revolutum (31, 263, 264, 436)
Notocotylus attenuatus (263, 436)
Tracheophilus cucumerinus (662)
Tracheophilus cymbium (37)
Typhlocoelum cucumerinum (282)
reticulare (241, 258, 259, 263)

CESTODA

Hymenolepis megalops (182, 262)
Hymenolepis terrae-reginae (182, 262)

'Anseres'

Cestodes (651)
Acanthocephala (651)
Unclassified worms (651)

Anseriformes

ARTHROPODA

MALLOPHAGA

Anaticola tordae (231)

ACANTHOCEPHALA

Filicollis sp. (97)

CESTODA

Fimbriaria sp. (97)
Hymenolepis aequabilis (181)
anatina (181)
arcuata (181)
biaculeata (181)
bilateralis (181)
bisaccata (181)
clausa (181)
collaris (181)
compressa (181)
conscripta (181)
coronula (181)
creplini (181)
diorchis (181)
echinocotyle (181)
fallax (181)
fasciculata (181)
flagellata (181)
fragilis (181)
gracilis (181)
groenlandica (181)
jägerskioldi (181)
kowalewskii (181)
lanceolata (181)
liophallos (181)
macracanthos (181)
macrocephala (181)
megalhystera (181)
megalops (181)
micrancristrota (181)
microsoma (181)
Hymenolepis octacantha (181)
orthocantha (181)
pachycephala (181)
parviceps (181)
parvula (181)
pigmentata (181)
przewalskii (181)
querquedula (181)
rarus (181)
retracta (181)
riggenbachi (181)
rosseteri (181)
sagitta (181)
setigera (181)
sibirica (181)
simplex (181)
solowiowi (181)
tenerrima (181)
tenuirostris (181)
teresoides (181)
terraereginae (181)
trichorhynchus (181)
trifolium (181)
tritesticulata (181)
venusta (181)
villosoides (181)
voluta (181)
Raillietina cyrtis (sic) (14)
parviuncinata (14)
anatina (14)
(Skrjabinia) microcotyle (14)

Aythya affinis (Eyton), Lesser Scaup

PROTOZOA

Leucocytozoon (159, 223, 455)

ARTHROPODA

MALLOPHAGA

Anaticola cornicephalus (231)
crassicorne (571)
Anatoecus dentatus (571)
Trinoton querquedulae (571)

ACARINA

Rhinonyssus rhinolethrum (573)

Aythya affinis (*cont.*)

TREMATODA

Amphimerus elongatus (194, 195)
Apatemon gracilis (144)
Cotylurus brevis (142, 144)
flabelliformis (142, 194, 195, 446)
Dendritobilharzia pulverulenta (479)
Echinostoma revolutum (194)
Levinseniella minuta (194, 195, 481)
Maritrema nettae (195)
Maritreminoides nettae (491)
Microbilharzia chapini (49, 195, 479, 578)
Prosthogonimus rudolphii (130, 194, 195)
Psilostomum marilae (483)
Sphaeridiotrema globulus (194, 195, 482)
Typhlocoelum cymbium (194, 195)
Zygocotyle lunata (482)
lunatum (194, 195)

CESTODA

Diorchis acuminata (182, 529)
excentricus (521)
Diploposthe laevis (37, 182, 521)
Fimbriaria fasciolaris (521)
Hymenolepis coronula (521)
echinorostrae (528)
Hymenolepis gracilis (521)
hamulacanthos (182)
jägerskioldi (521)
nyrocae (521)
tenerrima (521)

NEMATODA

Microfilariae (516, 653)
Ruzguniella kofoidi (661)
Tetrameres crami (195, 588)

Aythya americana (Eyton), Redhead

PROTOZOA

Leucocytozoon (223, 455, 671)

TREMATODA

Amphimerus elongatus (195)
Cotylurus flabelliformis (195)
Pseudobilharzia horiconensis (51)
Typhlocoelum cucumerinum (195)
Zygocotyle lunatum (195, 288, 478)

CESTODA

Cestodes not named (365)
Diorchis acuminata (344)
ransomi (37)
Diploposthe laevis (37, 486*b*, 521)
Fimbriarioides sp. (486*b*)
Hymenolepis hamulacanthos (195, 241, 344)
spp. (635)
Hymenolepis (Weinlandia) sp. (344)

Aythya australis australis (Eyton), Australian White-eye

ARTHROPODA

MALLOPHAGA

Anaticola nyrocae (231)

CESTODA

Diorchis flavescens (182, 195, 261, 381, 402, 529)
Diploposthe laevis (182, 260, 261, 262, 263, 589)
tuberculata (178)
Hymenolepis megalops (262)
Taenia laevis (175)
trichosoma (175)
tuberculata (305)

Aythya baeri (Radde), Baer's Pochard

PROTOZOA

Haemoproteus danilewskyi (40, 223, 471, 472)
Haemoproteus sp. (105)

Aythya baeri (*cont.*)

ARTHROPODA

ACARINA

Freyana anatina nyrocae (136)
Freyana largifolia nyrocae (136)

CESTODA

Diploposthe laevis (37, 182, 566)

Aythya collaris (Donovan), Ring-necked Duck

PROTOZOA

Haemoproteus nettionis (163)
sp. (223, 428)
Leucocytozoon sp. (223, 428, 454, 455)

ARTHROPODA

ACARINA

Freyana anatina nyrocae (136)
Freyana largifolia nyrocae (136)

TREMATODA

Cotylurus flabelliformis (194, 195)
Echinostoma revolutum (194)
Prosothogonimus rudolphii (130, 194, 195)
Pseudobilharzia burnetti (51)
waubesensis (51)

Aythya ferina (L.), European Pochard

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (43)
fuligulae (231)
Anatoecus dentatus (43)
difficilis (231)
Holomenopon nyrocae (231)
Menopon nyrocae (43)
Trinoton nyrocae (231)
querquedulae (43)

ACARINA

Freyana anatina nyrocae (136)
Freyana largifolia nyrocae (136)

TREMATODA

Amphimerus anatis (67)
Apatemon gracilis (141, 194, 195, 594)
gracilis minor (142)
gracilis var exilis (141)
Bilharziella polonica (37, 67)
Catatropis verrucosa (351, 437)
Cotylurus cornutus (37, 67, 142, 145*)
hebraicus (67)
Cyclocoelum arcuatum (194, 195, 282)
Dendritobilharzia pulverulenta (67)
Echinoparyphium clerci (67)
paracinctum (67)
recurvatum (37, 67)
Echinostoma revolutum (37, 67, 129)
Echinostomum revolutum (351, 437)
Hypoderaeum conoideum (37, 67, 129, 351, 437)
Hyptiasmus coelonodus (662)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 67, 194, 195)
Opisthorchis anatis (676)
Parastrigea robustus (67)
Philophthalmus nyrocae (194, 195)
Plagiorchis sp. (67)
Prosthogonimus probably cuneatus (54)
ovatus (130, 194, 195)
sp. (130, 351, 437)
sp. cuneatus (130)

Aythya ferina (*cont.*)

TREMATODA (*cont.*)

Psilochasmus longicirratus (242)
Renicola mediovitellata (66, 67, 675)
Schistogonimus rarus (67)
sp. (130)
Sphaeridiotrema globulus (67)
Strigea erratica (437)
Tanaisia fedtschenkoi (67)
Tetracotyle ardea (sic) (67)
Tracheophilus cymbium (37, 67)
Typhlocoelum cucumerinum (37, 67)

CESTODA

Anomotaenia ciliata (138)
Aploparaksis elisae (122)
furcigera (37, 122, 138, 351)
Apora dogieli (138)
Dicranotaenia coronula (122)
Diorchis acuminata (122)
inflata (122, 138)
mathevosianae (122)
nyrocae (138)
parvogenitalis (37, 122, 137, 138)
ransomi (37, 122)
Diorchis (Diorchis) parvogenitalis (393)
Diploposthe laevis (37, 137, 138, 178, 182, 195, 248, 283, 351, 566, 678)
skrjabini (137)
Drepanidotaenia bilateralis (122)
lanceolata (122, 182, 283, 351)
spinulosa (122, 138)
Fimbriaria fasciolaris (37, 137, 138, 182, 232)
Haploparaksis elisae (182, 195, 283)
Hymenolepis anatina (122)
arcuata (122, 182, 241, 283)
bisacculata (122)
collaris (37, 178, 182, 241, 283, 351, 552)
compressa (37, 122, 138, 195, 241)
coronula (37, 138)
Hymenolepis fallax (122, 182, 241, 283)
fasciata (182)
fasciculata (122, 241, 283)
fimula (122, 241, 410)
formosa (122, 138)
fragilis (138, 182, 283)
furcigera (178, 182, 283)
gracilis (122, 138, 182, 241, 283)
krabbeella (122, 241)
lanceolata (178, 195, 241)
macracanthos (122)
macrocephala (37, 122)
megalops (37, 138)
octacantha (122, 138)
paracompressa (122)
paramicrosoma (122, 138)
setigera (122, 178, 182, 195, 241, 283, 351, 410)
skrjabini (37, 138, 393)
solowiowi (122, 182, 241, 283)
sp. (122, 497)
spiralbursata (122)
trichosoma (182, 283)
wisniewskii (122)
Ligula intestinalis (37)
Orlovilepis megalops (122)
Taenia trichosoma (175, 336)

NEMATODA

Amidostomum fuligulae (382)
skrjabini (23, 25, 26)
Capillaria anatis (350)
spinulosa (195, 369, 625)
Echinocoleus spinulosus (350)
Echinuria fissispina (195, 288)
uncinata (37)
Tetrameres spinosa (26)

ACANTHOCEPHALA

Echinorhynchus anatis (391)
filicollis (391)
polymorphus (390)
striatus (390, 391)
Filicollis anatis (288, 351)
Polymorphus anatis (195)
minutus (37, 351, 415)
striatus (195, 351, 415)

Aythya fuligula (L.), Tufted Duck

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (43)
Anatoecus dentatus (43)
Anatoecus obtusus (231)
Trinoton querquedulae (43)

Aythya fuligula (*cont.*)

ARTHROPODA (*cont.*)

SIPHONAPTERA

Ceratophyllus garei (509)

ACARINA

Freyana anatina (486*c*)
anatina nyrocae (136)
Freyana largifolia largifolia (136)

TREMATODA

Apatemon fuligula (512)
fuligulae (194, 195, 446, 676, 680)
gracilis fuligulae (142)
gracilis minor (142)
gracilis var. exilis (141)
Bilharziella polonica (37, 195, 437, 441, 442, 479, 591)
Catatropis verrucosa (297, 437)
Cotylurus brevis (141, 142, 145)
cornutus (512)
Cryptocotyle concava (27, 437)
concavum (663)
Cyclocoelum arcuatum (194, 195, 282)
Distomum brachysomum (336)
globulus (55, 56, 351)
oxyurum (336)
Echinoparyphium recurvatum (194, 195, 214, 288, 351, 437, 511)
Echinostoma baculus (129)
recurvatum (129, 676)
revolutum (31, 37, 194, 195, 676)
Echinostomum sp. ? revolutum (437)
Eucotyle zakharowi (194, 195, 556)
Hypoderaeum conoideum (27, 288)
Hyptiasmus coelonodus (662)
Hyptiasmus laevigatus (297, 437, 663)
robustus (297, 437)
sp. (662)
Levinseniella pellucida (194, 195, 351, 437)
propinqua (27)
Maritrema subdolum (27)
Monostomum attenuatum (215)
flavum (375)
robustum (351)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 194, 195, 437, 676, 679)
Ophthalmophagus robustus (194, 195)
Opisthorchis simulans (191, 195)
Paramonostomum alveatum (27)
Prosthogonimus sp. (130)
Psilochasmus longicirratus (512, 680)
oxyurus (27, 67, 191, 194, 195, 351, 437, 549)
Psilostomum spiculigerum (56)
Schistogonimus rarus (67, 511)
Spelotrema pygmaeum (27)
Sphaeridiotrema globulus (194, 195, 437, 482)
Tracheophilus cucumerinum (662)
Typhlocoelum cucumerinum (37, 67, 194, 195, 282, 297, 437)

CESTODA

Aploparaksis fuligulosa (562)
Dicranotaenia coronula (122, 511)
coronula subsp. micracantha (393)
pseudocoronula (393)
Diorchis nyrocae (138)
parvogenitalis (138, 393)
Diploposthe laevis (37, 138, 178, 182, 195, 351, 566)
Drepanidotaenia lanceolata (122)
Fimbriaria fasciolaris (37, 138, 182, 406, 511, 512, 566)
Haploparaksis furcigera (182, 195)
Hymenolepis abortiva (122, 241)
anatina (122, 182, 241)
arcuata (122)
collaris (182, 195, 351, 552)
compressa (138, 182, 241, 552, 629*b*)
coronula (138)
Hymenolepis fallax (122, 138, 182, 241)
formosa (122, 138)
gracilis (566)
kowalewski (sic) (195, 241)
kowalewskii (122, 182)
megalops (178, 182, 195, 241, 351)
megarostellis (562)
nitidulans (195)
paramicrosoma (122, 241)
setigera (182, 241)
sinuosa (178)
sp. (562)
tenuirostris (122, 195, 241, 351)
upsilon (182)
villosoides (182, 241, 562)
Microsomacanthus microsoma (511)
Orlovilepis megalops (122)
Tschertkovilepis setigera (511)

Aythya fuligula (*cont.*)

NEMATODA

Amidostomum acutum (195, 627)
anseris (195, 555, 627)
boschadis (512)
fuligulae (382)
skrjabini (23, 26, 637)
Capillaria contorta (369, 374)
nyrocinarum (369)
Capillaria sp. (682)
spinulosa (369)
Epomidiostomum orispinum (195, 627)
Streptocara crassicauda (512)
Tetrameres fissispina (512)
fissispinus (511)
Thominx anatis (511, 512)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (45, 288)
Polymorphus anatis (195)
Polymorphus magnus (511)
minutus (38, 195, 415)

DIOCTOPHYMOIDEA

Eustrongylides mergorum (512)

Aythya marila marila (L.), European Greater Scaup

PROTOZOA

Leucocytozoon simondi (386)
Leucocytozoon sp. (159, 223, 471, 472)

ARTHROPODA

ACARINA

Freyana anatina nyrocae (136)

TREMATODA

Acanthoparyphium marilae (194, 195)
Catatropis verrucosa (351, 437)
Cotylurus brevis (141, 142)
cornutus (37, 194, 594)
flabelliformis (194, 195)
Cryptocotyle concava (437, 494)
concavum (351)
Distomum globulus (351)
Echinoparyphium baculus (194, 195)
recurvatum (37, 194, 195, 214, 288, 351, 437)
Echinostoma baculus (129)
revolutum (31, 129, 194, 195, 256)
Echinostomum baculus (347)
revolutum (347)
Hypoderaeum conoideum (37, 129, 194, 195, 347, 351)
Monilifer spinulosus (129)
Monostomum flavum (375)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 437)
Paramonostomum alveatum (194, 195, 297, 351, 437)
Prosthogonimus cuneatus (54, 130, 437)
ovatus (194, 195)
sp. (130, 351)
Psilochasmus oxyurus (194, 195, 351, 437, 549)
Psilostomum oxyurum (56)
Sphaeridiotrema globulus (194, 195, 437)
Stephanoprora spinosa (437)
Strigea erratica (437)
tarda (351, 437)
Tocotrema concavum (195)
Tracheophilus cucumerinus (662)
cymbium (37)
Typhlocoelum cucumerinum (37, 194, 195, 283, 297, 437)
flavum (351)

CESTODA

Dicranotaenia coronula (393)
kutassi (393)
Diorchis nyrocae (532, 678)
parvogenitalis (37)
Diploposthe laevis (37, 178, 182, 195, 283, 351)
Fimbriaria fasciolaris (37, 178, 182, 195, 283, 351)
Hymenolepis aequabilis (178, 182, 241, 283, 351)
arcuata (178, 182, 195, 241, 283, 351)

Aythya marila marila (*cont.*)

CESTODA (*cont.*)

Hymenolepis compressa (37, 182, 195, 241, 283, 351, 552)
coronula (37, 178, 182, 195, 241, 283, 351)
fallax (178, 182, 241, 283, 351)
gracilis (37, 178, 182, 195, 241, 283, 351)
megalops (37, 178, 182, 195, 241, 283, 351, 494)
microsoma (178, 182, 195, 241, 283, 351)
nitidulans (241)
nyrocae (241, 678)
pigmentata (178, 182, 195, 241, 283, 351)
Hymenolepis sacciperium (241, 402)
sacciperum (sic) (182)
sp. (178)
tenerrima (178, 182, 195, 241, 283)
tenuirostris (178, 195, 241, 351)
tritesticulata (182, 241, 283)
villosoides (241, 283)
Lateriporus skrjabini (393)
Schistocephalus gasterostei (241)
solidus (37, 195)
Strigea tarda (351)
Taenia pigmentata (334)
tenuirostris (490)

NEMATODA

Amidostomum anseris (195, 627)
skrjabini (23, 27, 627)
Capillaria nyrocinarum (369)
Capillaria spinulosa (369)
Tetrameres crami (195)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)
Polymorphus marilis (98, 195)
minutus (37, 195, 351, 415)

Aythya marila mariloides (Vigors), Pacific Greater Scaup

ARTHROPODA

MALLOPHAGA

Anatoecus dentatus (571)

TREMATODA

Acanthoparyphium kurogamo (680)
spinulosum (680)
suzugamo (680)
Cotylurus brevis (145)
Paramonostomum bucephalae (680)

CESTODA

Diorchis nyrocae (529)
Diploposthe laevis (376, 484†)
Fimbriaria fasciolaris (494†)
Hymenolepis aequabilis (494†)
arcuata (494†)
compressa (494†)
coronula (37, 494†)
fallax (494†)
gracilis (494†)
Hymenolepis kenaiensis (523)
megalops (494†)
microsoma (494†)
nyrocae (195)
pigmentata (494†)
sp. (494†)
tenerrima (494†)
tenuirostris (494†)
testiculata (344)

NEMATODA

Tetrameres crami (588)

Aythya novae-seelandiae (Gmelin), New Zealand Scaup or Black Teal

TREMATODA

Cercaria longicauda (effected experimental infection with this, but no adult trematodes found) (357)

† In 'Marila marila'.

Aythya nyroca (Güldenstädt), Common White-eye or Ferruginous Duck

PROTOZOA

Haemoproteus sp. (225, 303)
Leucocytozoon (455)

ARTHROPODA

MALLOPHAGA

Anatoecus icterodes (621)

ACARINA

Freyana anatina nyrocae (136)
Freyana largifolia nyrocae (136)

TREMATODA

Bilharziella polonica (37, 194, 195, 479)
Cotylurus cornutus (37)
Echinoparyphium recurvatum (37)
Echinostoma sp. (129)
Echinostomum sp. (? revolutum) (37, 351, 437)
Hypoderaeum conoideum (37)
Metorchis hovarkai (361)
Notocotylus attenuatus (512)
Psilochasmus longicirratus (437, 549)
Psilochasmus simillimum (440)
Psilotrema simillimum (194, 195, 351, 437, 440)
spiculigerum (194, 195, 351, 437, 442)
Strigea tarda (351, 437)
sp. (37)
variegata (437)
Typhlocoelum cucumerinum (37)

CESTODA

Anomotaenia ciliata (37)
Aploparaksis elisae (195, 554)
Diorchis inflata (37)
nyrocae (512)
Diploposthe laevis (37, 175, 178, 182, 351, 554)
Drepanidotaenia lanceolata (182, 351)
Fimbriaria fasciolaris (554)
Hymenolepis collaris (37)
compressa (37, 552, 554)
coronula (37)
lanceolata (178, 241)
megalops (37, 178, 182, 241, 351, 554)
solowiowi (195)

NEMATODA

Amidostomum anseris (555)
boschadis (512)
Epomidiostomum uncinatum (382, 627)
Porrocaecum crassum (37)
Tetrameres gynaecophila (195)
sp. (555)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)
minutus (37, 38)

Aythya sp.

ACANTHOCEPHALA

Corynosoma semermе (415)

Aythya vallisneria (Wilson), Canvasback

PROTOZOA

Leucocytozoon (223, 454, 455)

ARTHROPODA

MALLOPHAGA

Acidoproctus kelloggi (231)

Aythya vallisneria (*cont.*)

TREMATODA

Amphimerus elongatus (194, 195)
Cotylurus flabelliformis (194, 195)
Microbilharzia canadensis (49, 362)
Microbilharzia manitobensis (49, 362)
Pseudobilharzia kegonensis (49)

CESTODA

Diorchis longae (521, 529)
nyrocae (346)
wigginsi (532)
Hymenolepis compressa (37, 97, 178, 182, 241, 494, 552)
fusus (97)
Taenia compressa (343)

NEMATODA

Microfilariae (653)

Biziura lobata (Shaw), Musk Duck

PROTOZOA

Plasmodium biziurae (107, 188, 228)
Proteosoma biziurae (262)

TREMATODA

Echinostoma revolutum (264)

CESTODA

Taenia moschata (178, 260, 305, 589)

NEMATODA

Amidostomum biziurae (276, 614)
Tetrameres biziurae (276)

Branta bernicla bernicla (L.), Russian or Dark-bellied Brent Goose

ARTHROPODA

MALLOPHAGA

Anatoecus natatorum (231)
Docophorus brevimaculatus (621)

TREMATODA

Catatropis verrucosa (27)
Monostomum verrucosum (215)
Notocotylus attenuatus (297, 437)
Notocotylus imbricata (194)
Paramonostomum alveatum (27, 195, 297, 437)

CESTODA

Drepanidotaenia lanceolata (182, 283)
Hymenolepis bilateralis (241, 342)
Hymenolepis lanceolata (178, 195, 241, 494)
setigera (178, 241, 283, 494)

ACANTHOCEPHALA

Echinorhynchus polymorphus (390)
Polymorphus minutus (37, 195, 415)

Branta bernicla hrota (O. F. Müller), Atlantic or Light-bellied Brent Goose

PROTOZOA

Tyzzeria anseris (211)

Branta bernicla orientalis Tougarinov, Pacific Brent Goose or Black Brant

NEMATODA

Amidostomum spp. (635)

Branta canadensis canadensis (L.), Atlantic Canada Goose

PROTOZOA

Eimeria sp. (545, 650)
striata (165)
truncata (165, 166)
Haemoproteus nettionis (650)
sp. (220, 223, 225, 653)
Leucocytozoon simondi (650)
Leucocytozoon sp. (159, 220, 223)
Trichomonas anseri (sic) (650)
Trypanosoma sp. (128)
Tyzzeria fulva (165)
hermani (165)
sp. (164, 545, 650)

ARTHROPODA

MALLOPHAGA

Ornithobius atromarginatus (231)
Trinoton anserinum (151)

ACARINA

Sternostoma rhinolethrum (692)

TREMATODA

Apatemon gracilis (144)
gracilis canadensis (142, 146)
'Blood flukes' (650)
Catatropis harwoodi (63)
Hypoderaeum conoideum (73)
Notocotylus attenuatus (650)
Ornithibilharzia pricei (49, 654)
Paramonostomum brantae (63)
Prosthogonimus sp. (650)
Psilochasmus longicirratus (73)
Renicola brantae (675)
Trichobilharzia brantae (167)
Zygocotyle lunatum (73)

CESTODA

Cestodes not identified (365)
Diploposthe laevis (37, 178, 182, 494)
Drepanidotaenia lanceolata (650)
megalops (521)
Fimbriaria sp. (486*b*)
Hymenolepis sp. (486*b*, 650)
sp. (probably lanceolata) (486*b*)

NEMATODA

Amidostomum anseris (111*, 113, 226, 255, 650, 658)
spatulatum (226, 627, 644)
sp. (227)
Capillaria sp. (650)
Cyathostoma brantae (114)
Echinuria parva (114, 658)
uncinata (290)
Epomidiostomum crami (627, 644, 655)
Heterakis circumvallata (633)
dispar (195)
Microfilariae (9, 658)
Tetrameres sp. (650)
Trematodes not named (365)
Trichostrongylus tenuis (120, 374, 650)

Branta canadensis hutchinsii (Richardson), Richardson's Canada Goose

PROTOZOA

Eimeria anseris (211)
brantae (211)
Eimeria magnalabia (211)

Branta canadensis interior Todd, Central or Todd's Canada Goose

PROTOZOA

Eimeria anseris (211)
fulva (211)
hermani (211)
magnalabia (211)
truncata (211)
Haemoproteus anatis (225)
Haemoproteus sp. (328)
Leucocytozoon simondi (328)
sp. (455)
Plasmodium (probably circumflexum) (328)
Tyzzeria anseris (211)
sp. (324, 325)

TREMATODA

Renicola brantae (360)

NEMATODA

Microfilariae (328)

Branta canadensis leucopareia (Brandt), Aleutian Canada Goose

PROTOZOA

Eimeria brantae (165)

Branta canadensis minima Ridgway, Cackling Canada Goose

PROTOZOA

Eimeria hermani (211)
magnalabia (211)
Leucocytozoon (223)
Tyzzeria anseris (211)

CESTODA

Hymenolepis barrowensis (524)

NEMATODA

Cyathostoma brantae (114)

Branta canadensis moffitti Aldrich, Great Basin or Moffitt's Canada Goose

PROTOZOA

Tyzzeria anseris (211)

Branta canadensis parvipes (Cassin), Lesser Canada Goose

PROTOZOA

Eimeria brantae (211, 326, 462)
'Coccidian oocysts' (327)

Branta canadensis taverni Delacour, Taverner's Canada Goose

PROTOZOA

Tyzzeria anseris (211)

Branta leucopsis (Bechstein), Barnacle Goose

ARTHROPODA

MALLOPHAGA

Anatoecus brunneopygus (231)
Ornithobius hexopthalmos (231)

Branta leucopsis (*cont.*)

ARTHROPODA (*cont.*)

SIPHONAPTERA

Ceratophyllus vagabunda insularis (509)
Ceratophyllus lunatus (510)

TREMATODA

Catatropis verrucosa (437)
Notocotylus attenuatus (437)

CESTODA

Hymenolepis longivaginata (176*d*, 178, 182, 241, 283, 494)
Hymenolepis setigera (178, 182, 195, 241, 283, 494)

NEMATODA

Amidostomum anseris (195, 627)
spp. (635)
Epomidiostomum orispinum (195, 627)
Heterakis dispar (195)

Branta ruficollis (Pallas), Red-breasted Goose

ARTHROPODA

MALLOPHAGA

Anatoecus brantae (231)

Branta sandvicensis (Vigors) Hawaiian Goose or Ne-Ne

NEMATODA

Capillaria anseris (369)
Heterakis dispar (195, 371)
Streptocara crassicauda (195)

Bucephala albeola (L.), Bufflehead

ARTHROPODA

ACARINA

Freyana anatina bucephalae (136)

Bucephala clangula americana (Bonaparte), American Goldeneye

PROTOZOA

Haemoproteus nettionis (163)
Leucocytozoon sp. (223, 428)

TREMATODA

Amphimerus elongatus (195)
Apatemon gracilis (73, 195)
gracilis fuligulae (142)
Catatropis verrucosa (195)
Cloacitrema ovatum (195)
Cotylurus flabelliformis (142, 195)
Cryptocotyle concava (495)
Cyclocoelum arcuatum (195)
Echinoparyphium baculus (195)
Levinseniella brachysoma (195)
Maritrema nettae (195)
Maritreminoides nettae (194, 491)
Notocotylus imbricata (195)
Paramonostomum bucephalae (195)
Prosthogonimus cuneatus (195)
rudolphii (130, 194)
Psilochasmus oxyurus (195)
Spelophallus bucephalae (195)
Spelotrema pygmaeum (195)
Stephanoprora spinosa (195)

Bucephala clangula americana (*cont.*)

CESTODA

Diploposthe laevis (195, 494)
Fimbriaria fasciolaris (195, 494)
Hymenolepis coronula (195, 344, 494)
macracanthos (195, 494)

NEMATODA

Amidostomum anseris (195)
Capillaria anatinis (398)
Contracaecum micropapillatus (195)
spiculigerum (195)
Epomidiostomum sp. (195)
Streptocara crassicaudum (195)
Tetrameres crami (195, 588)

Bucephala clangula clangula (L.), European Goldeneye

PROTOZOA

Eimeria bucephalae (94, 370, 462)
Leucocytozoon sp. (455)

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (43)
Anatoecus dentatus (43)
Anatoecus icterodes (621)
Trinoton luridum (616)

ACARINA

Freyana anatina bucephalae (136)

TREMATODA

Apatemon gracilis (142, 194, 594)
gracilis var. exilis (141)
Bilharziella polonica (37, 67)
Catatropis verrucosa (194, 297, 351, 437)
Cloacitrema ovatum (194, 677)
Cryptocotyle concava (370, 437)
concavum (351, 663)
Cyclocoelum arcuatum (194, 282)
mutabile (437)
Dicrocoelium eurysternum (437)
Distomum brachysomum (336)
eurystomum (351)
Echinochasmus japonicus (680)
Echinoparyphium baculus (194)
flexum (486*b*)
Echinostoma baculus (129)
revolutum (37)
Echinostomum revolutum (437)
sp. (351)
Hypoderaeum conoideum (37, 288)
Hyptiasmus arcuatus (297, 437, 662)
Levinseniella brachysoma (194, 437)
propinqua (27)
sp. (351)
Monostomum arcuatum (351)
Notocotylus attenuatus (37, 67)
Paramonostomum bucephalae (194, 677)
Prosthogonimus cuneatus (130, 194, 351, 437)
sp. (130)
Psilochasmus oxyurus (194, 351, 437, 549)
Spelophallus bucephalae (194, 677)
Stephanoprora spinosa (437)
Strigea erratica (437)
tarda (437)
Tocotrema concavum (194)

CESTODA

Diploposthe laevis (37, 178, 283, 351)
Fimbriaria fasciolaris (37, 137, 138, 178, 283, 351)
Hymenolepis aequabilis (241)
compressa (37)
coronula (27, 37, 138, 178, 182, 241, 283, 351)
fallax (283)
Hymenolepis macracanthos (138, 178, 241, 283, 349, 351)
mayhewi (232, 241, 283)
monoposthe (138)
pittulagai (241, 283)
Lateriporus skrjabini (138)
Ligula intestinalis (37, 283)
Taenia macracanthos (335)
Weinlandia (Hymenolepis) mayhewi (629*b*)

Bucephala clangula clangula (*cont.*)

NEMATODA

Amidostomum anseris (555, 627)
skrjabini (27)
Capillaria contorta (374)
mergi (369)
Capillaria nyrocinarum (369)
spinulosa (369)
Epomidiostomum orispinum (627)
Streptocara crassicauda (555)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351, 415)
Polymorphus matthevosianae (468)
minutus (415)

Bucephala islandica (Gmelin), Barrow's Goldeneye

ARTHROPODA

MALLOPHAGA

Anaticola clangulae (231)

ACARINA

Freyana anatina bucephalae (136)

NEMATODA

Avioserpens bifidus (447)

Cairina hartlaubi hartlaubi (Cassin), Western Hartlaub's Duck

NEMATODA

Acuaria uncinata (635)

Cairina moschata (L.), Muscovy Duck

PROTOZOA

Haemoproteus sp. (105, 227, 323)
Leucocytozoon simondi (86)

ARTHROPODA

MALLOPHAGA

Anaticola cairinensis (231)
Holomenopon cairinae (231)
Holomenopon transvaalense (231)
Lipeurus crassicornis (270)

ACARINA

Freyana moschatae (136)
Freyana subanatina (136)

TREMATODA

Amphistoma lunatum (575)
Apatemon globiceps (142)
graciliformis (142, 194, 195, 594)
sphaerocephalus (194, 195, 594)
Echinostoma mendax (129)
revolutum (31, 194, 195, 354)
Metorchis coeruleus (56, 194, 195, 419, 639)
xanthosomus (130)
Ophthalmophagus magalhaesi (195, 639, 662
Prosthogonimus sp. (130)
Spaniometra magalhaesi (282)
Tracheophilus cymbium (37)
obovale (662)
Typhlocoelum cucumerinum (282)
obovale (639)
Zygocotyle lunatum (194, 195, 288, 626, 639)

Cairina moschata (*cont.*)

CESTODA

Biuterina longiceps (178, 195, 494)
Diorchis flavescens (529)
Drepanidotaenia lanceolata (182, 488)
Fimbriaria fasciolaris (37, 182)
Lateriporus biuterinus (178, 179, 494)
Hymenolepis bisaccata (178, 182, 195, 241, 494)
lanceolata (178, 241, 494)
megalops (37, 178, 182, 241, 494)
papillata (178, 182, 195, 241, 494)

NEMATODA

Ascaridia galli (195, 456)
Capillaria anatis (456)
cairinae (369)
caudinflata (373, 374, 456)
Eucoleus cairinae (350)
Heterakis dispar (371, 195)
Oxyspirura parovatum (195)
Porrocaecum crassum (37, 195)
Streptocara formosensis (579, 580)
Trichostrongylus tenuis (374)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)

Cairina moschata dom.

PROTOZOA

Plasmodium cathemerium (668*)
elongatum (668*)
Plasmodium lophurae (668*)
relictum (668*)

CESTODA

Fimbriaria fasciolaris (494)

Cairina moschata—cross breeds of, in Formosa

NEMATODA

Streptocara formosensis (580)

Cairina scutulata (S. Müller), White-winged Wood Duck

PROTOZOA

Haemoproteus (303)

Cereopsis novae-hollandiae (Latham), Cereopsis or Cape Barren Goose

ARTHROPODA

MALLOPHAGA

Anaticola australis (231)
Lipeurus australis (269)

CESTODA

Fimbriaria intermedia (410)

NEMATODA

Heterakis dispar (371)
Heterakis papillosa (25, 26, 383)

Chenonetta jubata Latham, Australian Wood Duck or Maned Goose

NEMATODA

Cyathostoma sp. (205)
Heterakis chenonettae (262, 272, 371)

Chloephaga melanoptera (Eyton), Andean Goose

NEMATODA

Acuaria streperina (270)

Chloephaga picta leucoptera (Gmelin), Falkland Upland or Greater Magellan Goose

ARTHROPODA

MALLOPHAGA

Anaticola marginellus (231)
Lipeurus marginellus (617)

Chloephaga picta picta (Gmelin), Upland or Lesser Magellan Goose

NEMATODA

Amidostomum sp. (635†)

Chloephaga poliocephala Sclater, Ashy-headed Goose

NEMATODA

Amidostomum anseris (195, 627)
Heterakis acuticaudata (371)

Clangula hyemalis (L.), Long-tailed Duck or Old Squaw

PROTOZOA

'Coccidium oocysts' (327)
Haemoproteus nettionis (163)
Leucocytozoon sp. (159)
'Oocysts, possibly Eimeria parvula and Tyzzeria sp.' (326)

ARTHROPODA

MALLOPHAGA

Anaticola frater (231)
Anatoecus natatorum (231)

ACARINA

Freyana anatina oidemiae (136)

TREMATODA

Apatemon gracilis (594)
gracilis minor (16)
'glacialis' (sic) (195)
Catatropis verrucosa (27, 194, 195, 297, 351, 437)
Cyathocotyle prussica (142, 195, 351, 425, 437)
Cryptocotyle concava (437, 494)
concavum (351, 663)
Cyclocoelum arcuatum (194, 195, 282)
Distomum globulus (351)
platyurum (425)
Hypoderaeum conoideum (37, 288)
Gymnocephalus choledocus (387)
Hyptiasmus laevigatus (297, 437, 662)
Levinseniella brachysoma (194, 195, 437)
sp. (351)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 194, 195, 437)
Ornithodiplostomum ptychocheilus (142)
Paradiplostomum ptychocheilus (195, 634)
Paramonostomum alveatum (194, 195, 297, 351, 437)
Prosthogonimus ovatus (130, 194, 195, 288, 351, 437)
Psilochasmus oxyurus (194, 351, 437, 549)
Psilostomum brevicolle (56, 194, 195, 437, 440, 442)
platyurum (351)
Sphaeridiotrema globulus (194, 437, 482)

† In 'Upland' or Magellan Goose.

Clangula hyemalis (*cont.*)

TREMATODA (*cont.*)

Strigea erratica (437)
tarda (351, 437)
variegata (437)
Tocotrema concavum (195)
Tracheophilus cucumerinus (662)
cymbium (37)
Trematode eggs not identified (326)
Typhlocoelum cucumerinum (37, 194, 195, 282, 297, 437)

CESTODA

Aporina borealis (342)
Cestode eggs not identified (326)
Choanotaenia borealis (178, 194, 494)
sp. (21)
Diagonaliporus spasskyi (307)
Fimbriaria falciformis (37, 195, 283, 344)
fasciolaris (27, 178, 182, 195, 283, 351, 494)
Fimbriariella lintoni (643)
Fimbriarioides falciformis (182)
intermedia (527)
Haploparaksis groenlandica (16)
Hymenolepis coronula (16, 37, 241, 494)
diorchis (27)
groenlandica (178, 182, 195, 241, 283, 494)
Hymenolepis jägerskioldi (527)
megalhystera (178, 182, 283, 342)
microsoma (178, 182, 241, 283, 342, 351, 494)
paramicrosoma (521)
sp. A (21)
sp. B (21)
tenuirostris (387)
Lateriporus geographicus (376)
laevis (178)
teres (182, 283, 351, 494, 527)
Notobothrium arcticum (342)
Schistocephalus gasterostei (351)
solidus (37, 195, 283)

NEMATODA

Capillaria anatis (195, 350, 625)
mergi (369)
nyrocinarum (369)
spp. (398)
Echinocoleus spinulosus (350)
Echinuria borealis (400)
Streptocara crassicauda (195)

ACANTHOCEPHALA

Corynosoma strumosum (195)
Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351, 415)
Polymorphus anatis (195)
minutus (195, 415)

DIOCTOPHYMOIDEA

Eustrongylides mergorum (195)

Coscoroba coscoroba (Molina), Coscoroba Swan

CESTODA

Hymenolepis megalops (178, 182, 241)
Hymenolepis orthacantha (176*d*, 178, 182, 241)

NEMATODA

Cyathostoma coscoroba (79)

Cyanochen cyanopterus (Rüppell), Abyssinian Blue-winged Goose

ARTHROPODA

ACARINA

Freyana anatina cyanocheni (136)
Freyana largifolia cyanocheni (136)

Cygnus atratus (Latham), Black Swan

PROTOZOA

Plasmodium (Proteosoma) biziurae (263)
Plasmodium biziurae (102)
Plasmodium sp. (107)

ARTHROPODA

MALLOPHAGA

Anatoecus megaceros (231)
Colpocephalum castaneum (269)
caudatum (616)
Cicinophilus castaneus (231)
Docophorus cygni (621)
Lipeurus anatis megaceros (269)
squalidus var. atrata (618)
Ornithobius cygni (620)
fuscus (231, 269)
sp. (413)
Trinoton conspurcatum (616)
niger (269)
nigrum (231)

TREMATODA

Apatemon fuhrmanni (141, 142)
intermedius (142, 266)
Echinoparyphium ellisi (265)
gizzardi (636)
sp. (636)
Echinostoma revolutum (31, 263, 264, 436)
Hemistomum intermedium (257, 259, 260, 589)
Hyptiasmus magnus (259, 662)
Monostomum sp. (260, 262)
Notocotylus attenuatus (259, 263, 436)

CESTODA

Diorchis spiralis (529, 532, 606)
Drepanidotaenia bisacculina (182, 606)
curiosa (182, 606)
lanceolata var. lobata (182)
Echinorhynchotaenia nana (385, 402)
Hymenolepis bisaccata (606)
bisacculina (241)
curiosa (241)
globosa (182)
Hymenolepis globulosa (241, 606)
lanceolata (385, 566)
lanceolata spotanskiaca (241)
liophallos (241, 260, 262)
micrancristrota (241, 260, 262)
rapida (182, 241, 606)
southwelli (182, 241)
sp. (262, 566)

NEMATODA

Amidostomum cygni (276)
Capillaria circumvallata (260, 262)
ellisi (275)
Heterakis dispar (371)
Heterakis gallinae (195, 260)
gallinarum (371)
vesicularis (262, 555, 623)
Tetrameres australis (273)

Cygnus columbianus bewickii Yarrell, Bewick's Swan

ARTHROPODA

MALLOPHAGA

Anatoecus cygni (231)
Anatoecus sp. (413)

Cygnus columbianus columbianus (Ord), Whistling Swan

PROTOZOA

Haemoproteus sp. (223, 225, 653)
Trypanosoma sp. (128)
Tyzzeria anseris (211)

ARTHROPODA

MALLOPHAGA

Ornithobius cygni (571)

Cygnus columbianus columbianus (*cont.*)

CESTODA

Hymenolepis lanceolata (521)
Hymenolepis sp. (521)

NEMATODA

Amidostomum cygni (627, 645)
Sarconema eurycerca (486*a*, 486*b*, 648)

Cygnus columbianus jankowskii Alpheraky, Eastern Bewick's or Jankowski's Swan

TREMATODA

Catatropis cygni (680)
Notocotylus parviovatus (680)

Cygnus cygnus buccinator Richardson, Trumpeter Swan

ARTHROPODA

MALLOPHAGA

Anaticola pallidus (231)
Lipeurus jejeunus (617)
Ornithobius cygni (110)

TREMATODA

Echinostoma revolutum (110)
Orchipaedum tracheicola (110)
Zygocotyle lunatum (110)

CESTODA

Hymenolepis (Drepanidotaenia) bisacculina (284)
Hymenolepis spp. (110)

NEMATODA

Sarconema eurycerca (110)

Cygnus cygnus cygnus (L.), Whooper Swan

ARTHROPODA

MALLOPHAGA

Anatoecus icterodes (621)
musicus (231)
Docophorus cygni (619, 621)
Ornithobius bucephalus (619, 620)
cygni (231)
Trinoton conspicuratum

TREMATODA

Catatropis verrucosa (351, 437)
Echinostoma paraulum (437)
revolutum (37, 129, 331, 351, 437)
sp. (437)
Holostomum exiguum (351, 437)
Lyperosum sp. (331)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 437)
Paramonostomum alveatum (195, 297, 351, 437)
Prosthogonimus cuneatus (54, 130, 195, 288, 351, 437)
Strigea tarda (351. 437

CESTODA

Drepanidotaenia lanceolata (182, 283)
setigera (104)
Hymenolepis aequabilis (108, 178, 182, 195, 241, 283, 351)
creplini (108, 178, 182, 241, 283, 351)
lanceolata (178, 195, 241)
Hymenolepis liophallos (178, 182, 241, 283, 351)
megalops (37, 178, 182, 195, 241, 283, 351)
micrancristrota (178, 182, 195, 241, 283, 351)
setigera (178, 182, 195, 241, 283, 351)

Cygnus cygnus cygnus (*cont.*)

NEMATODA

Ascaris spiculigera (104)

ACANTHOCEPHALA

Filicollis anatis (288, 351)
Polymorphus anatis (195)
Polymorphus minutus (195, 351)

Cygnus cygnus dom.

ACANTHOCEPHALA

Polymorphus minutus (37)

Cygnus ferus

ACANTHOCEPHALA

Echinorhynchus filicollis (391)

Cygnus melanocoryphus (Molina), Black-necked Swan

PROTOZOA

Plasmodium relictum (535)
Plasmodium sp. (107)

ARTHROPODA

MALLOPHAGA

Anatoecus brevithoracicum (231)
Lipeurus jejeunus (617)
Menopon brevithoracicum (615)
Ornithobius sp. (413)

CESTODA

Hymenolepis megalops (37)

NEMATODA

Capillaria drummondi (350, 369, 625)
Epomidiostomum vogelsangi (627)
Tetrameres fissispina (195, 288)

Cygnus olor (Gmelin), Mute Swan

PROTOZOA

Eimeria truncata (93)

ARTHROPODA

MALLOPHAGA

Anatoecus sp. (413)
Docophorus cygni (621)
Ornithobius bucephalus (621)

ACARINA

Freyana anserina (486*c*)

HIRUDINEA

Protoclepsis granata (152)

Cygnus olor (*cont.*)

TREMATODA

Apatemon fuhrmanni (140, 141)
gracilis fuhrmanni (142)
Bilharziella polonica (37, 49, 195, 479)
Catatropis verrucosa (437)
Cotylurus cornutus (27, 142)
strictus (152)
Echinoparyphium recurvatum (565)
Echinostoma revolutum (129)
sp. (129)
Echinostomum revolutum (37, 351, 437)
sp. (437)
Gigantobilharzia monocotylea (152)
Ophyrocotyle minutum (152)
Paramonostomum alveatum (351, 437)
Pseudobilharziella filiformis (603)
Psilostomum cygnei (sic) (567)
Sphaeridiotrema globulus (195, 437, 482)

CESTODA

Hymenolepis aequabilis (152, 178, 182, 195, 241, 283, 351, 494)
anatina (182, 195, 241, 283, 488)
creplini (178, 182, 241, 283, 351, 494)
fona (241, 410)
gracilis (567)
lanceolata (494)
Hymenolepis liophallos (494)
megalops (494)
micrancristrota (494)
setigera (182, 195, 241, 283, 494)
Hymenolepis (Drepanidotaenia) bisacculina (284)
Nematoparataenia paradoxa (183)
southwelli (283)

NEMATODA

Amidostomum similis (611)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
polymorphus (390)
striatus (351, 391)
Filicollis anatis (37, 288, 351, 415, 567)
Polymorphus anatis (195)
minutus (351, 415)
striatus (195, 415)

Cygnus olor dom., Domesticated Mute Swan

ARTHROPODA

MALLOPHAGA

Anatoecus icterodes (621)
Lipeurus crassicorne (270)
Ornithobius bucephalus (231)
Ornithobius cygni (270)
fuscus (270)
Trinoton cygni (231)

CESTODA

Hymenolepis aequabilis (178, 351, 494)
anatina (178, 351, 494)
Hymenolepis setigera (178, 351, 494)

NEMATODA

Acuaria uncinata (421)
Echinuria uncinata (37, 195)

ACANTHOCEPHALA

Filicollis anatis (37, 351, 415)
Polymorphus minutus (195, 351, 415)
Polymorphus striatus (415)

Cygnus sp.

TREMATODA

Cyathostoma bronchialis (79)
Dendritobilharzia sp. (329)

NEMATODA

Amidostomum anseris (399

Dafila spinicauda ? *Anas* sp.

CESTODA

Hymenolepis megalops (37)

Dendrocygna arborea (L.), Black-billed or Cuban Whistling Duck

ARTHROPODA

MALLOPHAGA

Acidoproctus maximus (231, 620)
Trinoton lituratum (616)

Dendrocygna arcuata arcuata (Horsfield), East Indian Wandering Whistling Duck

ARTHROPODA

MALLOPHAGA

Acidoproctus maximus (620)
Lipeurus luridus (619)

ACARINA

Freyana dendrocygni dendrocygni (136)

CESTODA

Diorchis flavescens (182, 529)
Diplogynia oligorchis (13, 182)
Hymenolepis spp. (635)

Dendrocygna arcuata australis Reichenbach, Australian Wandering Whistling Duck

CESTODA

Diorchis flavescens (381)
Diploposthe laevis (262, 263)
Ophiotaenia hylae (381)

Dendrocygna autumnalis autumnalis (L.), Northern Red-billed Whistling Duck

ARTHROPODA

ACARINA

Freyana dendrocygni dendrocygni (136)

CESTODA

Lateriporus biuterinus (178, 179, 182, 494)

Dendrocygna autumnalis discolor Sclater & Salvin, Southern Red-billed Whistling Duck

ARTHROPODA

MALLOPHAGA

Acidoproctus hopkinsi (231)

NEMATODA

Cyathostoma sp. (635)

Dendrocygna bicolor (Vieillot), Fulvous Whistling Duck

PROTOZOA

Haemoproteus sp. (206)

ARTHROPODA

ACARINA

Freyana dendrocygni dendrocygni (136)

CESTODA

Diorchis sp. (17)
Hymenolepis sp. A (17)
Hymenolepis sp. B (17)

NEMATODA

Filariasis. Adult worms not identified (203)

Dendrocygna eytoni (Eyton), Plumed or Eyton's Whistling Duck

ARTHROPODA

ACARINA

Freyana dendrocygni dendrocygni (136)

NEMATODA

Porrocaecum streperae (270)

Dendrocygna guttata Schlegel, Spotted Whistling Duck

ARTHROPODA

ACARINA

Dendrocygna furculasetae (136)

Dendrocygna javanica (Horsfield), Lesser or Indian Whistling Duck

PROTOZOA

Haemoproteus danilewskyi (473)

ARTHROPODA

ACARINA

Freyana dendrocygni dendrocygni (136)

TREMATODA

Ornithobilharzia sp. (190)
Paryphostomum testrifolium (190)
Petasiger minutissimus (190)

CESTODA

Cittotaenia sandgroundi (125)
Hymenolepis clausa (178, 182, 241, 341, 409, 566)
Hymenolepis coronula (37, 182)
javanensis (126)

Dendrocygna viduata (L.), White-faced Whistling Duck

ARTHROPODA

MALLOPHAGA

Acidoproctus bifasciatus (620)
rostratus (231, 460)
Holomenopon dendrocygni (460)
Trinoton aculeatum (231)

ACARINA

Freyana dendrocygni dendrocygni (136)
Speleognathus womersleyi (460)

TREMATODA

Echinostoma mendax (129)
revolutum (31)
Opisthorchis geminus (41)
Trichobilharzia sp. (156)

CESTODA

Hymenolepis sp. (286)

NEMATODA

Acuaria uncinata (635)

Domestic duck (including *Anas platyrhynchos platyrhynchos dom.* and White Pekin Ducks and experimental infections of these)

PROTOZOA

Cochlosoma anatis (299)
Eimeria truncata (165, 461)
Haemoproteus nettionis (163*)
sp. (89)
Hexamitus intestinalis (299)
Leucocytozoon simondi (85, 86, 89, 112*, 160*, 161, 239*, 386, 649)
sp. (192)
Plasmodium cathemerium (546*, 664*, 665*, 666*, 668*, 670*)
circumflexum (158*, 379*, 380)
elongatum (379*, 667*, 668*)
Plasmodium lophurae (33*, 158*, 240*, 253*, 668)
nucleophilum (379*)
relictum (665*, 668*)
relictum var. matutinum (379*)
Protrichomonas ? anatis (299)
'Sarcosporidia' (34)
Tetratrichomonas anatis (299)
Trichomastix gallinarum (299)
Trichomonas eberthi (299)
Tyzzeria perniciosa (7)

ARTHROPODA

MALLOPHAGA

Anaticola zunkeri (231)
Lipeurus anatis (270)
Menopon obscurum (270)

TREMATODA

Amphimerus elongatus (194, 195)
Apatemon fuligulae (194, 446)
gracilis (142)
gracilis japonicus (142)
japonicus (243, 244)
pellucidus (194, 195, 446, 676)
Bilharziella polonica (37, 194, 195, 592)
polonika (592)
yokogawai (420)
Cephalogonimus vesicaudus (8)
Clonorchis (Opisthorchis) sinensis (294)
Cotylurus attenuatus (243)
brevis (142)
cornutus (37, 142, 194, 195, 446)
flabelliformis (142, 194, 195)
japonicus (142, 243, 244)
Cyathocotyle orientalis (446)
ravieri (446)
Cyathocotyloides curonensis (446)
Diplostomum pelmatoides (496)
Echinochasmus beleocephalus chankensis (135)

Domestic duck (*cont.*)

TREMATODA (*cont.*)

Echinoparyphium recurvatum (37, 194, 351, 437, 630, 631, 685)
koidzumii (243, 244)
Echinostoma goroi (448)
minor (194)
miyagawai (243, 244)
pekinensis 1(94, 195)
revolutum (31, 129, 194, 195, 243, 244, 264, 420, 448, 501, 549, 630, 631, 638*, 676)
Echinostomum elongatum (194)
revolutum (351)
Hypoderaeum conoideum (22, 129, 194, 234, 414, 420, 437, 549, 638*, 685)
sinensis (194)
Levinseniella amnicolae (154)
Maritrema obstipum (154)
Metorchis crassiusculus (437)
orientalis (194, 234, 244, 685)
taiwanensis (234, 420, 685)
xanthosomus (351, 437)
Monostomum minutissimum (437)
Notocotyla attenuata (243)
Notocotyle intestinalis (631)
naviformis (631)
triserialis (351)
Notocotylus aegyptiaca (32)
aegyptiacus (194, 195, 437, 605)
anatis (194, 195, 308)
attenuatus (37, 194, 243, 244, 420, 437, 676, 685)
gibbus (194, 195)
intestinalis (194, 630)
naviformis (194, 630)
Ophryocotyle sp. (123)
Opisthorchis simulans (437)
tsingkiangpuensis (234)
Ornithodiplostomum pteichocephalus (446)
Paradiplostomum pteichocheilus (634*)
Paramonostomum ovatus (194)
parvum (194)
Paraphystomum horai (20)
Parastrigea robusta (194, 195)
Philophthalmus anatinus (130, 194, 420)
gralli (685)
razalensis (194, 630, 631)
sinensis (234)
Prosthogonimus anatinus (194, 195, 351, 437)
cuneatus (130, 310)
horiuchii (130, 194, 310, 420, 685)
japonicus (243, 244)
leei (130)
macrorchis (130, 194, 195)
orientalis (130, 310)
ovatus (130, 194)
pellucidus (130, 194, 195, 310)
penni (130, 310)
putschkowskii (130)
rudolphii (130, 194, 195)
sinensis (130, 310)
skrjabini (130, 194)
sp. plur. (130)
Pseudobilharziella yokogawai (194, 195)
Psilochasmus japonicus (244)
longicirratus (630, 631)
oxyurus (194, 195)
Psilostomum ondatrae (32)
Schistogonimus rarus (130)
Spelotrema pseudogonocotyla (83)
Strigea tarda (351, 437)
Tetracotyle sp. (97)
Tracheophilus cymbium (37)
hepaticus (420)
sisowi (420, 549, 551, 685)
Trichobilharzia elvae (367*)
kossarewi (364)
ocellata (109, 364*, 368)
oregonensis (367*, 368*)
stagnicolae (364*)
szidati (429)
Typhlocoelum cucumerinum (194)
cymbium (194, 282, 598)
obovale (639)
Zygocotyle lunatum (194, 195, 626)

CESTODA

Anomotaenia ciliata (37)
Aploparaksis filum (124)
furcigera (37, 122, 123)
stefańskii (122)
Cotugnia digonophora (566)
fastigata (566)
Davainea anatina (178, 351, 494)
sp. (97)
Dicranotaenia coronula (122)
coronula subsp. micracantha (393)
pseudocoronula (393)
Diorchis formosensis (529, 583)
stefańskii (122)
Diplopostthe laevis (37, 178, 182, 351, 494)
Drepanidotaenia coronula (507)

Domestic duck (*cont.*)

CESTODA (*cont.*)

Drepanidotaenia gracilis (507)
lanceolata (122, 182, 283, 351, 488)
Echinocotyle rosseteri (122, 182, 351, 494)
Fimbriaria fasciolaris (37, 123, 178, 182, 283, 351, 405, 494, 566, 583, 678)
Hymenolepis abortiva (182, 407, 488)
acicula (508)
anatina (122, 178, 182, 351, 494, 583, 685)
angularostris (122, 583)
bisacculata (122)
collaris (37, 178, 182, 283, 351, 488, 494, 552)
compressa (37, 122)
conscripta (283)
coronula (37, 123, 178, 182, 351, 404, 488, 494, 685)
fasciata (566)
fasciculata (283)
giransensis (122, 583)
gracilis (37, 122, 123, 178, 182, 283, 351, 488, 566, 583)
lanceolata (178, 494)
megalops (37, 178, 182, 351, 488, 494)
oshimai (583)
paracompressa (122)
Hymenolepis paramicrosoma (122)
parvula (122, 178, 182, 351, 488, 494)
rosseteri (178)
sagitta (122, 178, 182, 488, 494)
setigera (122, 182, 488, 583)
sphenocephala ((566)
tenuirostris (122, 178, 182, 283, 351, 488, 494)
venusta (182, 488, 494)
Hymenolepis (Weinlandia) collaris (583)
coronula (583)
megalops (583)
Kowalewskius yoshidai (683)
Ligula intestinalis (583)
Monopylidium infundibulum (562)
Raillietina anatina (182, 488)
Raillietina (Skrjabinia) microcotyle (182, 488)
Raillietina (Raillietina) parviuncinata (182, 566)
Schistocephalus solidus (37, 283)
Taenia anatina (508)
brachysoma (178)
conica (178)
conscripta (488)
Unciunia acapillicirrosa (195, 417)

NEMATODA

Acuaria uncinata (187)
Acuaria (Echinuria) uncinata (65)
Amidostomum anatinum (581)
anseris (115, 555, 632, 649)
skrjabini (23, 25)
Ascaridia galli (25, 195, 374)
lineata (195)
Capillaria anatis (369, 374)
caudinflata (374)
contorta (115, 118*a*, 184, 369, 374, 555, 649)
spp. (374, 398)
Cyathostoma bronchialis (115, 195, 572)
spp. (374)
Echinuria uncinata (37, 114, 195)
spp. (374)
Epomidiostomum anatinum (555)
uncinatum (25, 195, 627, 655)
spp. (374)
Eucoleus raillieti (350)
Heterakis beramporia (371, 374)
dispar (195, 371)
gallinae (195)
gallinarum (374)
isolonche (272, 371, 374)
lineata (555)
spp. (374)
vesicularis (555)
Microfilariae (89)
Porrocaecum crassum (25, 26, 37, 555)
sp. (374, 513)
Streptocara formosensis (579, 580)
Syngamus bronchialis (555)
trachea (372, 374, 375)
Tetrameres americana (116)
crami (116, 195, 586)
fissispina (115, 116, 195)
fissispinus (555)
gigas (195)
Trichostrongylus tenuis (119, 120, 195, 374, 649)

ACANTHOCEPHALA

Echinorhynchus polymorphus (390)
Filicollis anatis (37, 351, 610)
Polymorphus boschadis (123)
Polymorphus magnus (444, 467, 469)
minutus (37, 195, 351, 431, 444, 610)

Domestic duck (*cont.*)

DIOCTOPHYMOIDEA

Eustrongylides mergorum (195)
papilloides (195)
spp. (374)
tricolor (582)
Eustrongylides tubifex (195)
Hystrichis sp. (374)
tricolor (195, 289, 582, 610)

Domestic goose (including *Anser anser dom.*, when thus named, but excluding *A. anser anser*, when thus named)

PROTOZOA

Coccidium truncatum (489)
Eimeria anseris (165)
fulva (165)
hermani (165)
nocens (165, 300)
parvula (165, 300)
Eimeria striata (165)
truncata (165, 300, 489, 658)
Leucocytozoon anseris (106, 246, 293)
sp. (658)
Plasmodium gallinaceum (60*, 61*)
Tyzzeria anseris (438)

ARTHROPODA

MALLOPHAGA

Anaticola anseris (231)
Anatoecus adjustus (231)
Cicinophilus pectiniventris (231)
Holomenopon transvaalense (231)
Lipeurus crassicornis (270)
Trinoton conspicuratum (619)
squalidum (231)

ACARINA

Rhinonyssus rhinolethrum (573)
Rhinonyssus sp. (628)

TREMATODA

Bilharziella polonica (37, 218)
Catatropis verrucosa (351)
Cercarioides baylisi (427)
Echinoparyphium recurvatum (62, 218)
Echinostoma paraulum (218)
revolutum (31, 62, 129)
Echinostomum revolutum (351)
Hypoderaeum conoideum (62, 129, 218, 288, 351)
Metorchis taiwanensis (288)
Monostomum arcuatum (351)
Notocotyle attenuatus (62)
triserialis (351)
Notocotylus attenuatus (37, 218)
seineti (218)
thienemanni (218)
Prosthogonimus horiuchii (195)
ovatus (288)
sp. (351)
Zygocotyle lunata (478)
lunatum (626)

CESTODA

Aploparaksis furcigera (37)
Diploposthe laevis (37)
Drepanidotaenia lanceolata (169, 182, 351, 488)
Fimbriaria fasciolaris (37, 178, 182, 351, 494)
Hymenolepis collaris (37, 182, 351, 494, 552)
conscripta (37, 182)
fasciata (178, 351)
fasciculata (182, 488, 494)
gracilis (37, 178, 182, 351, 488, 494, 554)
Hymenolepis lanceolata (178, 494)
longicirrosa (629*b*)
longistylosa (629*b*)
pingi (629*b*)
setigera (488)
sinuosa (178)
tenuirostris (178, 182, 488, 494)
Taenia conscripta (488, 494)
krabbei (178, 351)
tenuirostris (487)

NEMATODA

Acuaria uncinata (187)
Agamospirura sp. (555)
Amidostomum anseris (76, 115, 195, 218, 295, 555, 649)

Domestic goose (*cont.*)

NEMATODA (*cont.*)

Amidostomum sp. (374)
Ascaridia galli (374)
Capillaria anatis (184, 350, 374, 625)
anseris (369)
caudinflata (373, 374)
skrjabini (627)
spp. (374)
Cyathostoma bronchialis (79, 115, 195, 197)
sp. (374)
Echinuria sp. (374)
uncinata (37, 114, 195)
Epomidiostomum orispinum (195, 627)
skrjabini (627)
sp. (374)
Eucoleus raillieti (350)
Heterakis dispar (194, 295, 371, 555)
gallinae (195)
gallinarum (371)
papillosa (490)
sp. (374)
Microfilariae (658)
Microtetrameres sp. (374)
Ornithofilaria fallisensis (9)
Streptocara sp. (374)
Syngamus bronchialis (555)
trachea (372, 374)
Tetrameres fissispina (288)
sp. (374)
Trichostrongylus tenuis (119, 120, 195, 374, 545, 649)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus corynoides (550)
minutus (351, 550)

DIOCTOPHYMOIDEA

Eustrongylides sp. (374)
Hystrichis sp. (374)
Hystrichis tricolor (289)

Ducklings not named (including experimental infections)

PROTOZOA

Leucocytozoon simondi (160, 649, 649*)
Plasmodium cathemerium (669*)
elongatum (669*)
Plasmodium lophurae (669*)
relictum (669*)
Tyzzeria perniciosa (649, 649*)

HIRUDINEA

Protoclepsis tesselata (377, 505)

TREMATODA

Apatemon fuligulae (676*)
Bilharziella polonica (479)
yokogawai (479)
Echinoparyphium petrowi (430*)
recurvatum (214*)
Echinostoma miyagawai (90*)
paraulum (90*)
revolutum (90*, 256)
Gigantobilharzia huronensis (149*)
Metorchis orientalis (233*)
taiwanensis (233*)
Microbilharzia chapini (578)
Notocotylus seineti (214*)
urbanensis (353)
Procerovum cheni (237*)
Prosthogonimus pellucidus (314*)
Psilochasmus longicirratus (233*)
Trichobilharzia adamsi (149*)
elvae (367)
oregonensis (367)
Xiphidocercariae not identified (214*)

CESTODA

Hymenolepis coronula (531)

NEMATODA

Echinuria uncinata (506)
Microfilariae (87)
Ornithofilaria fallisensis (10*, 11*)
Tetrameres fissispina (185, 477)

Ducklings not named (*cont.*)

ACANTHOCEPHALA

Polymorphus magnus (466)

DIOCTOPHYMOIDEA

Hystrichis tricolor (198)

'Ducks' not named (including experimental infections)

PROTOZOA

Eimeria spp. (649)
Haemoproteus sp. (239, 533)
Leucocytozoon anatis (106, 216, 453)
simondi (84, 162, 239*, 450, 649)
Leucocytozoon sp. (172, 451, 452, 455, 657)
Plasmodium cathemerium (664)
lophurae (313)
relictum (485)
Sarcocystis tenella (34*)

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (536)
ewingi (231)
Anatoecus icterodes (536)
Docophorus icteroides (619)
Docophorus platalea (619)
Menopon obscurum (536)
Nirmus argulus (620)

SIPHONAPTERA

Echidnophaga gallinacea (536)

ACARINA

Dermanyssus gallinae (536)
Liponyssus bursa (536)
Rhinonyssus rhinolethrum (573)
Sternostoma rhinolethrum (692)

IXODIDES

Argas persicus (536)

HIRUDINEA

Protoclepsis tesselata (377)

TREMATODA

Adult trematode not identified (109)
Amphimerus anatis (195, 593*)
Apatemon gracilis (593*)
japonicus (243)
Bilharziella polonica (117, 443, 591)
polonica, (eggs of) (59)
yokogawai (eggs and adult of) (59*)
Catatropis verrucosa (595)
Cephalogonimus sp. (195)
Clonorchis sinensis (294)
Cotylurus attenuatus (243)
cornutus (561, 595*)
flabelliformis (117)
Cyathocotyle fusa (245*)
gravieri (395)
Cyclocoelum pseudomacrostomum (195)
Echinochasmus beleocephalus chankensis (135)
Echinoparyphium flexum (195)
koidzumii (243)
recurvatum (561)
Echinostoma elongata (232)
elongatum (195)
lindoensis (45*)
minor (195)
miyagawai (243)
pekinensis (195)
revolutum (31, 44, 134, 232, 536, 576)
Hypoderaeum conoideum (561)
gnedini (544)
sinensis (195, 232)
vigi (544)
Maritrema rhodanicum (75*, 195)

'Ducks' not named (*cont.*)

TREMATODA (*cont.*)

Mehlisia gatesi (541)
Metorchis orientalis (195, 235*, 244*, 245, 608)
sp. (195, 219, 608)
taiwanensis (688)
Monostomum alveatum (52)
flavum (375)
Notocotyla attenuata (243)
Notocotyle gibbus (576)
Notocotylus anatis (195)
attenuatus (171, 394, 561, 595, 605)
imbricata (593)
intestinalis (195)
naviformis (195)
urbanensis (353)
Ophthalmophagus massinowi (195)
Paramonostomum ovatus (195, 232)
Paramonostomum parvum (195, 576)
Philophthalmus anatinus (195, 579)
razalensis (195)
Prosthogonimus horiuchii (195)
japonicus (243, 244)
leei (195, 232)
macrorchis (366*)
pellucidus (599)
skrjabini (195)
Psilochasmus oxyurus (171, 440, 442, 576, 602*)
Tracheophilus sisowi (133)
Trematodes not named (133, 365)
Trichobilharzia ocellata (59, 195)
sp. (155)
Typhlocoelum flavum (171)
neivae (195)
Zygocotyle lunata (660*)

CESTODA

Anomotaenia sphenoides (409)
Cestodes not identified (365)
Cotugnia fila (182, 409)
sp. (287)
Davainea sp. (97)
Diploposthe laevis (97, 279)
Drepanidotaenia lanceolata (2, 97, 281)
Echinocotyle rosseteri (376)
Fimbriaria fasciolaris (2, 281, 287, 536)
plana (514)
Hymenolepis abortiva (561)
anatina (2, 281, 287, 358, 561)
apcaris (541)
collaris (2, 561)
coronula (2, 281, 287, 561)
gracilis (2, 281, 358, 561)
infrequens (541)
Hymenolepis jamunica (541)
meggitti (541)
parvula (2)
rangoonica (541)
sp. (2)
tenuirostris (541)
Raillietina anatina (409)
cyrtus (195)
fecunda (409)
osakensis (247)
pseudocyrtus (409)
sp. (134, 287)
Raillietina (Parionella) fecunda (182)
Raillietina (Raillietina) pseudocyrtus (182)
Raillietina (Ransomia) parviuncinata (411)
Taenia sensu lato (286)
Weinlandia megalops (171)

NEMATODA

Acuaria uncinata (389)
sp. (134)
Amidostomum anseris (5*)
fuligulae (382)
skrjabini (25)
sp. (374, 449)
Ascaridia anatis (332)
galli (536)
lineata (358)
Capillaria anatis (171)
annulata (76)
contorta (76, 374, 649)
sp. (133, 134)
Contracaecum microcephalum (195)
Cosmocephalus sp. (374)
Cyathostoma bronchialis (649)
sp. (374)
Echinuria sp. (374)
uncinata (230, 290, 458, 658)
Echinuriasis (540)
Epomidiostomum sp. (374)
uncinatum (25, 382)
Filaria sp. (612)
uncinata (202)
Heterakis gallinae (5*, 536, 561)
Microfilariae (622)
Microtetrameres sp. (374)
Oxyspirura mansoni (536)
Porrocaecum crassum (332, 422, 423, 424)
ensicaudatum (374)

'Ducks' not named (*cont.*)

NEMATODA (*cont.*)

Pseudamidostomum boulengeri (25, 382)
Streptocara sp. (374)
Tetrameres americana (117, 195)
crami (195)
fissispina (117, 171, 195, 458, 561)
sp. (374)
Trichostrongylus tenuis (374, 561)

ACANTHOCEPHALA

'Acanthocephala' in a Pintail and Teal (365)
Corynosoma anatinarum (99)
constrictum (99)
Echinorhynchus polymorphus (97)
Filicollis anatis (133, 561)
Polymorphus boschadis (133, 358, 470)
magnus (444, 467, 469)
miniatus (195)
minutus (195, 332, 444)

DIOCTOPHYMOIDEA

Eustrongylides sp. (374)
Hystrichis sp. (374)
Hystrichis varispinosa (544)

Ducks, Wild, not named

PROTOZOA

Sarcocystis anatina (304)

TREMATODA

Cyclocoelum pseudomicrostomum (215, 662)
Hypoderaeum conoideum (542)
Ophthalmophagus massinowi (662)
Parastrigea anatis (67)

CESTODA

Hymenolepis cuneata (153, 182, 241)
makundi (547)
Raillietina (Raillietina) parviuncinata (182)

NEMATODA

'Gapeworm' not named (114)
Microfilaria (29)
Tetrameres crami (587)

ACANTHOCEPHALA

Filicollis anatis (610)
Polymorphus minutus (610)

DIOCTOPHYMOIDEA

Hystrichis tricolor (610)

'Fuligula contorta'

TREMATODA

Tracheophilus cucumerinus (662)

Geese not named

PROTOZOA

Eimeria anseris (649)
nocens (649)
parvula (649)
truncata (133)
Leucocytozoon simondi (162, 649)
Plasmodium sp. (503*)
Tyzzeria anseris (649)

ARTHROPODA

MALLOPHAGA

Anaticola anseris (536)
Anaticola crassicorne (530)

HIRUDINEA

Protoclepsis tesselata (377)
Theromyzon tesselatum (502)

Geese not named (*cont.*)

TREMATODA

Echinochasmus beleocephalus chankensis (135)
Echinoparyphium recurvatum (35)
Echinostoma elongata (232)
revolutum (157, 232, 539*)
Hypoderaeum sinensis (232)
Hyptiasmus sp. (642)
Notocotylus attenuatus (539, 605)
Opisthorchis anatis (232)
Paramonostomum alveatum (500, 642)
Paramonostomum ovatus (232)
Philopthalmus cupensis (500)
posavinensis (500)
Prosthogonimus cuneatus (500)
japonicus (232)
leei (232)
pellucidus (599)
sp. (642)
Ribeiroa ondatrae (291)
Trichobilharzia spp. (155)

CESTODA

Diploposthe laevis (97)
Drepanidotaenia lanceolata (292, 416, 536)
Drepanidotaenia sp. (457, 499, 537)
Hymenolepis tenuirostris (649)

NEMATODA

Amidostomum anserinum (133)
anseris (4, 5*, 35, 97, 254, 432, 538, 632, 686)
sp. (374, 449)
Ascaridia lineata (195)
Capillaria anatis (374)
contorta (118)
spp. (332)
Cyathostoma bronchialis (91, 649, 690)
sp. (374)
Echinuria uncinata (290, 458)
Epomidiostomum sp. (374)
Filaria uncinata (202)
'Gapeworm' (114)
Heterakis dispar (332)
gallinae (5*)
gallinarum (374)
spp. (374, 539)
Microtetrameres sp. (374)
Streptocara sp. (374)
Syngamus trachea (25)
Tetrameres bispinosa (651)
certa (651)
fissispina (458, 651)
globosa (651)
inermis (651)
paradoxa (651)
tenuis (651)
Trichostrongylus tenuis (374, 545)

DIOCTOPHYMOIDEA

Eustrongylides spp. (374)
Hystrichis spp. (374)

Goslings (including experimental infections)

PROTOZOA

Eimeria truncata (6, 168, 229, 330, 649)
Tyzzeria anseris (168)

TREMATODA

Echinoparyphium petrowi (430)

NEMATODA

Amidostomum anseris (168, 226, 356)
Ascaridia sp. (168)
Capillaria sp. (168)
Heterakis gallinae (168)

Histrionicus histrionicus histrionicus (L.), Atlantic Harlequin Duck

ARTHROPODA

ACARINA

Freyana anatina oidemiae (136)

Histrionicus histrionicus histrionicus (*cont.*)

TREMATODA

Notocotylus imbricata (195)

CESTODA

Hymenolepis pachycephala (178, 182, 241, 494)

Taenia pachycephala (334)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)

Histrionicus histrionicus pacificus W. S. Brooks, Pacific Harlequin Duck

ARTHROPODA

ACARINA

Freyana anatina oidemiae (136)

TREMATODA

Pseudospelotrema japonicus (680)

CESTODA

Hymenolepis pachycephala (681)

Lophonetta specularoides specularoides (King), Patagonian Crested Duck

NEMATODA

Acuaria uncinata (635)

Malacorhynchus membranaceus (Latham), Pink-eared Duck

ARTHROPODA

ACARINA

Freyana microchaeta (136)

Melanitta fusca deglandi (Bonaparte), American White-winged Scoter

ARTHROPODA

MALLOPHAGA

Anaticola constrictus (231)

TREMATODA

Dendritobilharzia sp. (49)
Distomum sp. A (345)
Himasthla incisa (194, 195, 345)
Orchipaedum tracheicola (81, 195)

CESTODA

Fimbriaria falciformis (344, 643)
fasciolaris (37, 182, 344)
plicata (97)
Fimbriariella 'lintoni new name' (643)
Fimbriarioides falciformis (182)
Hymenolepis tritesticulata (182, 344)
Hymenolepis (Weinlandia) sp. (344)

NEMATODA

Capillaria anatis (625)
Echinuria hypognatha (647)
Yseria californica (195)

Melanitta fusca dixoni (Brooks), Pacific White-winged Scoter

ARTHROPODA

MALLOPHAGA

Holomenopon loomisi (231)

TREMATODA

Cryptocotyle concava (495)

Melanitta fusca fusca (L.), Velvet or European White-winged Scoter

ARTHROPODA

MALLOPHAGA

Anaticola punctulatus (231)
Anatoecus natatorum (231)
Anatoecus roesleri (231)

TREMATODA

Apatemon gracilis (142, 194, 195, 594)
Catatropis verrucosa (297, 351, 437)
Cryptocotyle concava (437, 495)
concavum (351, 663)
Cyathocotyle melanittae (142, 194, 195)
prussica (142, 437)
Cyclocoelum arcuatum (195, 282)
Distomum piriforme (54)
Echinoparyphium baculus (194, 195)
Echinostoma baculus (129)
Echinostomum baculus (437)
Gymnophallus bursicola (194, 195)
dapsilis (194, 195, 433, 437)
Hyptiasmus laevigatus (297, 437, 662)
Monostomum flavum (375)
sp. (433)
Notocotyle triserialis (351)
Notocotylus attenuatus (194, 195, 437)
Orchipaedum tracheicola (37, 55, 56, 194, 195, 351, 437, 549)
Paramonostomum alveatum (194, 195, 297, 351, 437)
Psilostomum brevicolle (433, 437)
Renicola sp. (673, 675)
Spelotrema pygmaeum (433, 437, 492)
Strigea erratica (437)
gracilis (437)
tarda (351, 437)
Tocotrema concavum (194, 195)
Tracheophilus cucumerinus (662)
Typhlocoelum cucumerinum (37, 194, 195, 282, 297, 437)
flavum (351)

CESTODA

Dicranotaenia andrejowi (393)
pseudocoronula (393)
Diorchis bulbodes (182, 529)
Fimbriaria fasciolaris (37, 178, 182, 195, 283, 351, 494)
Hymenolepis coronula (37)
jägerskioldi (182, 241, 283)
Hymenolepis microsoma (178, 182, 195, 241, 283, 494)
tenuirostris (178, 182, 195, 241, 283, 494)
tritesticulata (241)
Lateriporus biuterinus (178, 182, 195, 283, 351, 494)
Taenia tenuirostris (487)

NEMATODA

Acuaria streperina (270)
Amidostomum acutum (195, 627)
anseris (195, 555, 627)
monodon (23)
skrjabini (627)
Capillaria anatis (195, 350)
Capillaria nyrocinarum (369)
mergi (369)
Epomidiostomum orispinum (195, 627)
Oxyspirura streparae (271)
Streptocara crassicauda (195)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)
minutus (37, 195, 351, 415)

Melanitta fusca stejnegeri (Ridgway), Asiatic White-winged Scoter

ARTHROPODA

ACARINA

Freyana anatina oidemiae (136)

TREMATODA

Apatemon fuligulae (195, 676)
gracilis fuligulae (594)
Echinostoma revolutum (37)

CESTODA

Fimbriaria fasciolaris (37)

Melanitta nigra americana (Swainson), American Black Scoter

ARTHROPODA

MALLOPHAGA

Trinoton minus (231)

TREMATODA

Acanthoparyphium marilae (680)
melanittae (680)
tyosenense (680)
Distomum flexum (97)
Echinostoma flexum (129)
Echinostoma revolutum (37)
Gymnophallus bursicola (680)
Pseudospelotrema japonicus (680)
Spelotrema pygmaeum (492)

CESTODA

Fimbriaria fasciolaris (37, 178, 182, 494)
Hymenolepis compressa (494)
microsoma (21)
Taenia macracantha (178, 182)
macrocantha (494)

ACANTHOCEPHALA

Echinorhynchus striatus (391)

Melanitta nigra nigra (L.), Common or Black Scoter

ARTHROPODA

MALLOPHAGA

Anaticola angustolimbatus (231)
Holomenopon lunarium (231)

SIPHONAPTERA

Ceratophyllus garei (509)

ACARINA

Freyana anatina oidemiae (136)

TREMATODA

Apatemon gracilis (194, 195, 594)
sp. (194)
Catatropis verrucosa (27, 194, 195, 435, 437)
Cryptocotyle concava (437)
concavum (662)
Cyclocoelum arcuatum (194, 283)
mutabile (437)
Distomum constrictum (437)
Echinoparyphium recurvatum (37, 258)
Echinostoma revolutum (37, 129, 194, 195, 250)
Echinostomum revolutum (351, 437)
Gymnophallus affinis (194, 195, 251)
bursicola (251, 437)

Melanitta nigra nigra (*cont.*)

TREMATODA (*cont.*)

Gymnophallus dapsilis (250, 251, 437)
dipsilis (? = dapsilis) (194, 195)
macroporus (194, 195, 251, 437)
oidemiae (194, 195, 251, 437)
ovoplenus (194, 195, 251, 437)
somateriae (250)
Himasthala (sic) incisa (194)
Holostomum crenulatum (437)
Hyptiasmus laevigatus (297, 437, 662)
Lecithodendrium somateriae (250)
Levinseniella brachysoma (194, 195, 251, 437)
Maritrema graciosum (27)
Metorchis xanthosomus (194, 195, 251, 437)
Monostomum sp. (250, 351)
Paramonostomum alveatum (27, 435, 437)
Psilochasmus oxyurus (194, 195, 250, 351, 437, 549)
Psilostomum brevicolle (194, 195, 250, 251, 433, 437)
Spelotrema pygmaea (250)
pygmaeum (27, 194, 195, 433, 434, 437)
Strigea gracilis (437)
tarda (250, 437)
Tocotrema concavum (251)

CESTODA

Diploposthe laevis (37, 178, 182, 195, 283, 351)
Fimbriarioides intermedia (182)
Hymenolepis compressa (37, 241, 552)
Hymenolepis micrancristrota (178, 182, 195, 283, 351)
microsoma (178, 182, 195, 241, 283, 351)

NEMATODA

Amidostomum acutum (195, 627)
anseris (195, 555, 627)
monodon (23, 27, 195, 555, 627)
skrjabini (627)
Capillaria nyrocinarum (369)
Epomidiostomum orispinum (195, 627)
uncinatum (195, 627, 655)
Microfilariae (534)
Strongylus monodon (336)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)

Melanitta perspicillata (L.), Surf Scoter

PROTOZOA

Haemoproteus nettionis (163)

ARTHROPODA

MALLOPHAGA

Anaticola constrictus (251)

ACARINA

Freyana anatina oidemiae (136)

TREMATODA

Distomum sp. B (345)

CESTODA

Fimbriaria falciformis (195, 344)
Fimbriariella lintoni (643)
Fimbriarioides falciformis (182)
Hymenolepis coronula (37, 182, 241)
tritesticulata (182, 241, 344)

ACANTHOCEPHALA

Filicollis altmani (465)

Melanitta sp.

CESTODA

Hymenolepis compressa (97)

Mergus albellus L., Smew.

ARTHROPODA

MALLOPHAGA

Anatoecus dentatus (43)
icterodes (621)
Trinoton lituratum (231)

ACARINA

Freyana anatina armata (136)

TREMATODA

Apatemon gracilis (141, 194, 195, 594)
gracilis minor (142)
Bilharziella polonica (37, 67, 437)
Cotylurus cornutus (37, 67)
erraticum (195)
ervaticus (194)
Cyclocoelum arcuatum (195, 282)
Distomum pusillum (67, 142)
Echinoparyphium baculus (194, 195, 351)
Echinostoma baculus (67, 129)
Hyptiasmus arcuatus (297, 437, 662)
Monostomum sp. (351)
Renicola sp. (673, 675)
Strigea erratica (351, 437)
gracilis (351, 437)
Tracheophilus cymbium (37)
Typhlocoelum cucumerinum (37, 194, 195, 282, 437, 662)
flavum (351)

CESTODA

Bothriocephalus ditremus (342)
Digramma interrupta (137)
Hymenolepis tenuirostris (178, 182, 195, 241, 283, 351, 494)
Ligula intestinalis (37, 137, 283, 351)
Paricterotaenia sp. (137)
Schistocephalus gasterostei (351)
solidus (37, 283)

NEMATODA

Echinuria uncinata (37)
Tetrameres inflata (624)
Tetrameres paradoxa (624)

ACANTHOCEPHALA

Echinorhynchus aluconis (391)
Centrorhynchus aluconis (195, 351, 415)

DIOCTOPHYMPIDEA

Eustrongylides mergorum (195)

Mergus cucullatus L., Hooded Merganser

PROTOZOA

Leucocytozoon sp. (223, 428)

ARTHROPODA

ACARINA

Freyana anatina lophodytes (136)

TREMATODA

Apatemon gracilis (142)
Ornithodiplostomum ptychocheilus (142)
Paradiplostomum ptychocheilus (195, 634)

Mergus cucullatus (*cont.*)

CESTODA

Diorchis sp. (521)
Hymenolepis aequablilis (521)
Hymenolepis querquedula (521)
simplex (521)

NEMATODA

Microfilariae (95)

ACANTHOCEPHALA

Polymorphus cucullatus (101)
Polymorphus sp. (96, 195, 415)

Mergus merganser americanus Cassin, American Merganser

PROTOZOA

Haemoproteus nettionis (163)
Leucocytozoon sp. (159, 223, 428)

TREMATODA

Monostomum attenuatum (215)
Ornithodiplostomum ptychocheilus (142, 446)
Stephanoprora mergi (73)

CESTODA

Diphyllobothrium ditremum (388)
Hymenofimbriaria merganseri (402)

NEMATODA

Capillaria anatis (625)
Contracaecum sp. (486*b*)
Contracaecum yamaguti (397)

ACANTHOCEPHALA

Polymorphus obtusus (484)

Mergus merganser merganser L., Goosander

ARTHROPODA

MALLOPHAGA

Anatoecus bipunctatus (231)
Lipeurus temporalis (617, 619)

ACARINA

Freyana anatina armata (136)

TREMATODA

Apatemon gracilis (141, 194, 195, 446, 594)
gracilis gracilis (141, 142)
Bilharziella polonica (15)
Catatropis verrucosa (297, 437)
Cryptocotyle concava (437)
concavum (351, 663)
Diplostomum parviventosum (27, 141, 142)
pelmatoides (141, 142)
pusillum (141, 142)
mergi (141, 142)
spathacum (27, 142)
Distomum globulus (351)
Echinoparyphium recurvatum (27)
Echinostoma sp. (129)
Hemistomum sp. (351)
Holostomum exiguum (351, 437)
Hypoderaeum anatis (288)
conoideum (37, 129, 194, 195, 351, 437)
Metorchis tener (195, 419)
Neodiplostomum orientale (194, 195)
Notocotyle triserialis (351)
Notocotylus attenuatus (194, 195, 297, 437)
Paradiplostomum ptychocheilus (195, 634)
Proalaria mergi (676)
Prosthogonimus cuneatus (288)
Sphaeridiotrema globulus (194, 437, 482)
Stephanoprora mergi (195)

Mergus merganser merganser (*cont.*)

TREMATODA (*cont.*)

Strigea erratica (351, 437)
gracilis (351, 437)
Tocotrema concavum (194, 195)
Tylodelphys excavata (37)

CESTODA

Digramma interrupta (232)
Diphyllobothrium ditremus (195, 351)
Fimbriaria fasciolaris (37, 178, 182, 195, 283, 351, 678)
Hymenofimbria merganseri (182, 195, 283)
Hymenolepis anceps (195)
coronula (37)
gracilis (37, 178, 182, 195, 241, 283, 351)
mergi (681)
Hymenolepis multistriata (241)
tenuirostris (178, 182, 195, 241, 283, 351)
tritesticulata (178, 182, 195, 241, 283, 351)
Ligula interrupta (487)
intestinalis (27, 37, 195, 351, 376)
Schistocephalus solidus (37, 195, 283, 351)
Taenia tenuirostris (487)

NEMATODA

Agamospirura sp. (555)
Ascaris sp. (larvae) (555)
Capillaria anatis (195, 350, 369)
mergi (369)
Contracaecum sp. (682)
Contracaecum spiculigerum (195, 555)
turkestanicum (195)
Streptocara crassicauda (195, 555)
Tetrameres fissispina (195, 288)

ACANTHOCEPHALA

Arythmorhynchus longicollis (193)
Echinorhynchus filicollis (391)
Corynosoma semerme (195, 415)
Corynosoma strumosum (195, 351)
Polymorphus anatis (195)
minutus (351)

DIOCTOPHYMOIDEA

Eustrongylides elegans (555)
mergorum (195, 682)
Hystrichis coronatus (195)

Mergus merganser orientalis Gould, Asiatic Goosander

CESTODA

Hymenofimbriaria merganseri (554)

Mergus octosetaceus Vieillot, Brazilian Merganser

ACANTHOCEPHALA

Echinorhynchus filicollis (391)

Mergus serrator serrator L., Red-breasted Merganser

PROTOZOA

Leucocytozoon anatis (621)
Leucocytozoon sp. (223, 238, 455, 671)

ARTHROPODA

MALLOPHAGA

Anaticola crassicorne (571)
mergiserrati (231)
Anatoecus dentatus (571)
icterodes (231)
Docophorus bipustulatus (621)
Trinoton mergi (231)
querquedulae (571)

SIPHONAPTERA

Ceratophyllus garei (509)

Mergus serrator serrator (*cont.*)

ARTHROPODA (*cont.*)

ACARINA

Freyana anatina (486*c*)
Freyana anatina arcuata (136)

TREMATODA

Apatemon gracilis (145, 194, 195, 594)
gracilis gracilis (142)
Austrobilharzia variglandis (463)
Catatropis verrucosa (194, 195, 351, 437)
Cryptocotyle concava (437)
concavum (351, 663)
Cyathocotyle prussica (141)
Diplostomum mergi (141, 142)
Distomum globulus (351)
Echinochasmus sp. (194, 195)
Heteroechinostomum sp. (437)
Holostomum exiguum (351, 437)
Maritreminoides ramunellae (127)
Metorchis coeruleus (219)
crassiusculus (194, 195)
pinguincola (219)
tener (219)
Metorchis xanthosomus (194, 195, 219)
Monostomum sp. (347)
Ophryocotyle insignis (348)
sp. (351)
Ornithodiplostomum ptychocheilus (142, 446)
Paradiplostomum ptychocheilus (145, 634)
Prosthogonimus rudolphii (195)
Sphaeridiotrema globulus (194, 195, 437, 482)
Stictodora japonica (680)
mergi (680)
Strigea gracilis (351, 437)
Tocotrema concavum (194, 195)
Typhlocoelum cucumerinum (37, 194, 195, 283, 437)
flavum (351)

CESTODA

Bothriocephalus ditremus (342)
Diorchis parviceps (178, 195, 261, 351, 402, 403, 494)
Diphyllobothrium ditremum (351)
ditremus (195)
Fimbriaria fasciolaris (37, 178, 182, 195, 283, 344, 351, 494)
Hymenolepis abortiva (241)
anceps (182, 241, 283, 344, 521)
coronula (37)
forma tadornae (351)
gracilis (37, 178, 182, 195, 241, 283, 351, 494)
lintoni (182, 241, 283, 349)
macracanthos (182, 241, 283, 349, 394)
maracanthoides (349)
Hymenolepis mergi (681)
parviceps (182, 241, 283)
spp. (635)
tenuirostris (108, 178, 182, 195, 241, 283, 351, 494)
tritesticulata (182, 241, 283, 394)
upsilon (182, 283)
Ligula intestinalis (37, 195, 283, 351)
Ophryocotyle insignis (195)
sp. (178, 182, 494)
Schistocephalus dimorphus (347, 348)
gasterostei (351)
solidus (37, 195, 283)
Taenia gracilis (348)
parviceps (334)
tenuirostris (348, 487)

NEMATODA

Ascaris sp. (347)
spiculigera (348)
Capillaria anatis (350, 625)
mergi (369)
Contracaecum spiculigerum (108)
Cosmocephalus obvelatus (195)
Microfilariae (671)
Streptocara crassicauda (195, 555)
Tetrameres inflata (624)

ACANTHOCEPHALA

Arhythmorhynchus frasoni (415)
frassoni (193, 195)
Corynosoma mergi (352)
semerme (351, 415)
strumosum (195, 351)
Echinorhynchus filicollis (391)
frasoni (391)
Echinorhynchus hystrix (347, 391)
striatus (351, 391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)
minutus (195, 351, 415)
striatus (195)

Mergus serrator serrator (*cont.*)

DIOCTOPHYMOIDEA

Eustrongylides mergorum (195) Hystrichis varispinosus (195)

Mergus sp.

ACANTHOCEPHALA

Corynosoma strumosum (415)

Mergus squamatus Gould, Chinese or Scaly-sided Merganser

ARTHROPODA

ACARINA

Freyana anatina armata (136)

Neochen jubatus (Spix), Orinoco Goose

ARTHROPODA

MALLOPHAGA

Lipeurus jejeunus (617)

TREMATODA

Echinostoma mendax (129) Echinostoma revolutum (31)

CESTODA

Lateriporus biuterinus (178, 179, 182)

NEMATODA

Acuaria uncinata (635)

Netta eryophthalma eryopthalma (Wied.), South American Pochard

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (460) Trinoton querquedulae (460)
Holomenopon sp. (460)

Netta peposaca (Vieillot), Rosybill

ARTHROPODA

ACARINA

Freyana anatina nyrocae (136) Freyana largifolia nyrocae (136)

CESTODA

Hymenolepis megalops (37) Hymenolepis sp. (635)

ACANTHOCEPHALA

Corynosoma peposacae (415) Echinorhynchus filicollis (391)

Netta rufina (Pallas), Red-crested Pochard

PROTOZOA

Haemoproteus sp. (105, 203, 225, 303)

ARTHROPODA

MALLOPHAGA

Acidoproctus moschatae (231)
stenopyx (231)
Trinoton querquedulae (43)

ACARINA

Freyana anatina nyrocae (136)
Freyana largifolia nyrocae (136)

TREMATODA

Cotylurus cornutus (512)
Echinostoma stromi (19)
Hypoderaeum conoideum (37)
Notocotylus attenuatus (418, 512)
Opisthorchis obsequens (67)
Psilochasmus skrjabini (189)
Trichobilharzia ocellata (512)

CESTODA

Anatinella meggitti (511)
Aploparaksis elisae (122)
furcigera (37, 554)
Diorchis danutae (122)
inflata (37, 122)
parvogenitalis (137)
ransomi (37, 122)
stefańskii (122)
Diorchis (Diorchis) nyrocae (122, 138)
Dicranotaenia coronula (122)
Diploposthe laevis (37, 137, 178, 182, 195, 283, 351, 494, 554)
Drepanidotaenia lanceolata (122, 182, 283, 351)
Fimbriaria fasciolaris (37, 137, 138, 178, 182, 283, 351, 494, 554)
Hymenolepis arcuata (122, 138)
bisaccata (122)
compressa (37, 122)
Hymenolepis coronula (37)
gracilis (37)
lanceolata (178, 195, 241, 494, 554)
macrocephala (122)
megalops (37, 138, 554)
monoposthe (138)
octacantha (122)
paracompressa (122)
paramicrosoma (122)
parvula (122)
rara (241, 283)
rarus (182, 194)
riggenbachi (182, 241, 283, 418)
solowiowi (122, 554)
spiralbursata (122)
teresoides (122)
Orlovilepis megalops (122)

NEMATODA

Acuaria uncinata (635)
Echinuria jugadornata (555)
Epomidiostomum anatinum (512)
Epomidiostomum uncinatum (26)
Thominx anatis (512)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus magnus (195, 415, 550)
minutus (37, 195)

Nettapus auritus (Boddaert), African Pygmy Goose

ARTHROPODA

ACARINA

Alloptes lambda (486*c*)
Freyana anatina (486*c*)
Freyana australis nettapina (136)

Nettapus coromandelianus cormandelianus (Gmelin), Indian Pygmy Goose or Cotton Teal

PROTOZOA

Haemoproteus danilewskyi (40, 225, 474) Haemoproteus sp. (105)

ARTHROPODA

ACARINA

Freyana australis australis (136)

CESTODA

Hymenolepis fista (410)

NEMATODA

Pseudamidostomum boulengeri (25, 26, 382, 627)

Nettapus pulchellus Gould, Green Pygmy Goose

ARTHROPODA

ACARINA

Freyana australis australis (136)

TREMATODA

Echinostoma revolutum (31, 263, 264) Notocotylus attenuatus (259, 263, 436)
Echinostomum revolutum (436)

Nettion delicata ?, *Anas*

TREMATODA

Zygocotyle lunatum (195)

Nyroca rufa (? *Aythya ferina* or *A. nyroca*)

CESTODA

Diploposthe sp. (392)

Oxyura dominica (L.), Masked Duck

TREMATODA

Echinostoma sp. (129)

Oxyura jamaicensis jamaicensis (Gmelin), North American Ruddy Duck

TREMATODA

Echinostoma multispinosa (464)

CESTODA

Diorchis excentricus (182, 195, 402, 403, 518, 521, 529, 532) Hymenolepis rauschi (518, 521)
Weinlandia cyrtoides (402)
Hymenolepis cyrtoides (182, 241)

Oxyura leucocephala (Scopoli), White-headed Stiff-tail

ARTHROPODA

MALLOPHAGA

Anaticola crassicornis (43)
Anatoecus dentatus (43)
Menopon nyrocae (43)
Trinoton querquedulae (43)

ACARINA

Bdellorhynchus polymorphus (486*c*)

TREMATODA

Cotylurus cornutus (37, 67)
Echinoparyphium clerci (67)
Echinostoma revolutum (67)
Notocotylus attenuatus (37, 67)

CESTODA

Diorchis (Nudiorchis) excentricus (138)
Diploposthe laevis (37, 176*a*, 178)
Drepanidotaenia gracilis (104)
lanceolata (138)
Fimbriaria fasciolaris (37, 104, 138, 178)
Hymenolepis coronula (37, 104, 178, 241)
gracilis (37, 178)
lanceolata (178, 241)
macracanthos (138)
megalops (37, 178, 241)

ACANTHOCEPHALA

Polymorphus minutus (37)

Plectropterus gambensis gambensis (L.), Spurwinged Goose

ARTHROPODA

MALLOPHAGA

Acidoproctus taschenbergi (460)
Anaticola asymmetricus (460)
gambensis (231)
Anatoecus sp. (460)
Holomenopon africanum (231)
Holomenopon albofasciatus (460)
tumidum (231, 460)
Lipeurus gambensis (617)
Menopon tumidum (615)

ACARINA

Freyana plectropteri (136)
Rhinonyssus rhinolethrum (460)
Sternostoma rhinolethrum (692)

TREMATODA

Opisthorchis geminus (41)
Tracheophilus cymbium (37)
Trichobilharzia sp. (156)
Typhlocoelum cucumerinum (37)

CESTODA

Hymenolepis octacantha (17)
Hymenolepis sp. (286)

Sarkidiornis melanotos carunculatus (Lichtenstein), South American Comb Duck

TREMATODA

Zygocotyle lunatum (195)

CESTODA

Lateriporus biuterinus (178, 179, 182)

Sarkidiornis melanotos melanotos (Pennant), Comb Duck

PROTOZOA

Haemoproteus sp. (105, 225, 504)

ARTHROPODA

MALLOPHAGA

Anaticola asymmetricus (460)
coloratus (231)
Holomenopon albofasciatum (460)
Holomenopon conei (231)
Lipeurus squalidus (617)
Trinoton sp. (460)

ACARINA

Freyana anatina sarkidiornis (136)
largifolia sarkidiornis (136)
Rhinonyssus rhinolethrum (460)

TREMATODA

Amphistoma lunatum (575)
Psilochasmus alii (249)
Tracheophilus cymbium (37)
sarcidiornicola (sic) (551)
Trichobilharzia sp. (156)
Typhultimum n.g. sarcidiornicola (sic) (662)
Zygocotyle lunatum (195, 639)

NEMATODA

Cyathostoma sarcidiornis (sic) (306)
Echinuria minor (515)
Epomidiostomum uncinatum (26, 382, 627)

Somateria fischeri (Brandt), Spectacled or Fischer's Eider

PROTOZOA

Plasmodium circumflexum (517)

CESTODA

Hymenolepis arctica (526)
Hymenolepis yukonensis (524)

Somateria mollissima borealis (C. L. Brehm), Northern Eider

TREMATODA

Apatemon gracilis (145)
Cotylurus brevis (145)
Lecithodendrium somateriae (250)

ACANTHOCEPHALA

Polymorphus botulus (100)

Somateria mollissima dresseri Sharpe, American Eider

NEMATODA

Amidostomum anseris (195, 627)

ACANTHOCEPHALA

Filicollis botulus (96, 97)
Polymorphus botulus (100, 195)
Profilicollis botulus (415)

Somateria mollissima mollissima (L.), European Eider

PROTOZOA

Eimeria bucephalae (165)
somateriae (93, 462)
Eimeria truncata (93, 462)

ARTHROPODA

MALLOPHAGA

Anaticola rubromaculatus (231)
Anatoecus icterodes (621)

SIPHONAPTERA

Ceratophyllus garei (509)

ACARINA

Sternostoma rhinolethrum (692)

TREMATODA

Apatemon gracilis (144)
gracilis var. somateriae (141)
Catatropis verrucosa (194, 195, 351, 437)
Cotylurus brevis (141, 142)
cornutus (37)
Cyclocoelum arcuatum (194, 195, 282)
Diplostomum mergi (141)
Distomum constrictum (437)
Gymnophallus bursicola (194, 195, 437, 439)
choledocus (194, 195, 347, 351)
somateriae (194, 195, 437, 439)
Hyptiasmus laevigatus (437, 662)
Levinsenia pygmaea (439)
Monostomum flavum (375)
sp. (347)
Notocotyle triserialis (351)
Notocotylus attenuatus (194, 195, 437)
Paramonostomum alveatum (194, 195, 351, 437)
Spelophallus primas (351, 437)
primus (194, 195)
Spelotrema pygmaeum (194, 195, 351, 434, 437, 492)
Strigea erratica (437)
tarda (351, 437)
Tracheophilus cucumerinus (662)
cymbium (37)
Typlocoelum cucumerinum (37, 194, 195, 282, 437)
flavum (351)

CESTODA

Aploparaksis murmanica (21)
Fimbriaria fasciolaris (37, 178, 182, 195, 283, 351, 494)
intermedia (402)
Fimbriarioides intermedia (182)
intermedius (283)
Haploparaksis murmanica (182, 283)
Hymenolepis diorchis (182, 241, 283)
fallax (178, 182, 195, 241, 283, 494)
jägerskioldi (241, 283)
Hymenolepis microsoma (178, 182, 195, 241, 283, 351, 494)
sp. (fragments of) (21)
tenuirostris (178, 182, 241, 283, 351, 494)
Lateriporus geographicus (182, 283)
teres (21, 177, 178, 182, 195, 283, 351, 494)
Taenia tenuirostris (487)
Tetrabothrium arcticus (494)
arcticum (182, 283)
Tetrabothrius arcticus (178, 195, 351)

NEMATODA

Amidostomum acutum (195, 627)
anseris (555, 627)
Capillaria nyrocinarum (369)
mergi (369)
Echinuria uncinata (37)
Epomidiostomum orispinum (195, 627)
Tetrameres inflata (624)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
lendix (351)
pupa (100)
Filicollis anatis (288, 351)
Polymorphus anatis (195)
boschadis (92)

Somateria mollissima mollissima (*cont.*)

ACANTHOCEPHALA (*cont.*)

Polymorphus botulus (100, 195, 415)
minutus (100, 195, 351, 415)
Polymorphus phippsi (195, 298, 415)

DIOCTOPHYMOIDEA

Eustrongylides mergorum (195)

Somateria mollissima v-nigra G. R. Gray, Pacific Eider

CESTODA

Hymenolepis arctica (526)

ACANTHOCEPHALA

Corynosoma mergi (100)
Polymorphus arcticus (100)

Somateria sp.

ARTHROPODA

ACARINA

Rhinonyssus rhinolethrum (573)

NEMATODA

Acuaria uncinata (635)

Somateria spectabilis (L.), King Eider

ARTHROPODA

MALLOPHAGA

Anaticola gracilis (231)

TREMATODA

Gymnophallus choledocus (387, 437)
deliciosus (387)
Gymnophallus somateriae (437, 439)
Spelotrema pygmaeum (387, 434, 437, 492)

CESTODA

Aploparaksis birulai (178, 182, 342, 494)
Diorchis sibirica (342, 532)
Fimbriaria fasciolaris (387)
Hymenolepis arctica (526)
macracantha (387)
Hymenolepis microsoma (178, 182, 241, 494)
retracta (178, 182, 241, 342, 494)
sibirica (178, 182, 241, 494)
tenuirostris (387)

NEMATODA

Amidostomum cygni (388)
Capillaria nyrocinarum (369)
Echinuria borealis (400)
uncinata (387)

ACANTHOCEPHALA

Echinorhynchus pupa (342)
Polymorphus arcticus (100, 195)
Profilicollis arcticus (387, 415)
Prosthorhynchus pupa (195, 415)

Somateria stelleri (Pallas), Steller's Eider

TREMATODA

Apatemon gracilis canadensis (142, 146)

CESTODA

Haploparaxis (sic) polystictae (526)

Stictonetta naevosa (Gould), Freckled Duck

ARTHROPODA

ACARINA

Freyana australis stictonettae (136)

Strepera versicolor (? = *Dendrocygna eytoni*, *Anas versicolor versicolor*, or *Strepera* of Passeriformes)

NEMATODA

Porrocaecum streperae (270)

Swan not named

ARTHROPODA

ACARINA

? Rhinonyssus rhinolethrum (573)

TREMATODA

Echinostoma revolutum (31) Notocotylus attenuatus (605)

CESTODA

Fimbriaria fasciolaris (609)

NEMATODA

Echinuria uncinata (114)

ACANTHOCEPHALA

Polymorphus boschadis (609)

Tachyeres brachypterus (Latham), Falkland Flightless Steamer Duck

ARTHROPODA

MALLOPHAGA

Anaticola breviceps (231)

Tachyeres patachonicus (King), Flying Steamer Duck

HIRUDINEA

Protoclepsis tesselata (505)

TREMATODA

Notocotylus tachyeretis (147, 605)

Tadorna cana (Gmelin), South African or Cape Shelduck

ARTHROPODA

MALLOPHAGA

Trinoton casarcae (231)

Tadorna ferruginea (Pallas), Ruddy Shelduck

ARTHROPODA

MALLOPHAGA

Lipeurus squalidus (617)

ACARINA

Freyana anatina casarcae (136)
Freyana anatina obliquasetae (136)

TREMATODA

Apatemon casarcus (640)
gracilis indicus (142)
indicus (640)
Lepoderma casarcii (412)
Lepoderma ferrugineum (412)
Petasiger longicirratus (309)
Prosthogonimus cuneatus (130, 558)

CESTODA

Diorchis flavescens (232, 529, 532)
Fimbriaria fasciolaris (410)
Hymenolepis echinocotyle (241, 410)

NEMATODA

Acuaria uncinata (635)
Epomidiostomum uncinatum (26, 382, 627)

Tadorna radjah radjah (Lesson), Moluccan or Black-backed Radjah Shelduck

ARTHROPODA

MALLOPHAGA

Acidoproctus bifurcatus (620)
Anaticola thoracicus (231)
Holomenopon obscurum (231)
Lipeurus thoracicus (617)
Trinoton intermedius (619)
intermedium (231)
lituratum var. intermedium (616)

ACARINA

Freyana anatina obliquasetae (136)
Freyana largifolia tadornae (136)

CESTODA

Hymenolepis lamellata (182, 295, 241)

Tadorna sp.

NEMATODA

Tetrameres fissispina (288)

Tadorna tadorna (L.), Common Shelduck

ARTHROPODA

MALLOPHAGA

Anaticola lacteus (231)
tadornae (231)
Anatoecus icterodes (621)
Colpocephalum quadriseriatum (231)
Docophorus icteroides (619)
Goniodes dissimilis (618)
Holomenopon albofasciatus (231)
tadornae (231)
Lipeurus lacteus (617, 619)
Menopon albofasciatum (615)

Tadorna tadorna (*cont.*)

ARTHROPODA (*cont.*)

ACARINA

Freyana anatina obliquasetae (136)

TREMATODA

Catatropis cygni (680)
verrucosa (27, 351, 437)
Echinostoma revolutum (31, 37, 129, 195)
Echinostomum revolutum (351, 437)
Gymnophallus choledocus (195, 351, 437, 439)
Hypoderaeum conoideum (37, 129, 351, 437)
Levinseniella brachysoma (27)
bucephalae (680)
Notocotyle triserialis (351)
Notocotylus attenuatus (37, 194, 195, 437)
Paramonostomum bucephalae (680)
Psilochasmus oxyurus (194, 195, 351, 549)
Strigea erratica (437)
tarda (351, 437)

CESTODA

Diorchis nyrocae (681)
Hymenolepis coronula (37, 178, 182, 195, 241, 283, 351)
gracilis (37, 178, 182, 195, 241, 283, 351, 681)
simplex (176*d*, 178, 182, 241, 283, 351)
Lateriporus destituta (182)
Paricterotaenia borealis (182, 283)
Taenia destituta (178, 347, 351)
gracilis forma tadornae (347)
sp. (347)
Taenia (s.l.) destituta (283)

NEMATODA

Acuaria uncinata
Ascaris sp. inq. (637)
Capillaria contorta (118, 369)
Cyathostoma tadornae (27)
Echinuria uncinata (37, 682)
Heterakis dispar (195, 371)
gallinae (195)
gallinarum (371)
vesicularis (555, 623)
Streptocara crassicauda (195)
tadornae (555)

ACANTHOCEPHALA

Echinorhynchus filicollis (391)
Filicollis anatis (37, 288, 351)
Polymorphus anatis (195)
minutus (195, 351, 415)

DIOCTOPHYMOIDEA

Hystrichis tricolor (37, 195)

Tadorna tadornoides (Jardine & Selby), Australian Shelduck

PROTOZOA

Haemoproteus danilewskyi (225, 262, 471, 472)

TREMATODA

Echinostoma revolutum (264, 268)

CESTODA

Hymenolepis lamellata (672)

NEMATODA

Syngamus trachealis (207)

Tadorna variegata (Gmelin), New Zealand Shelduck

ARTHROPODA

ACARINA

Freyana anatina obliquasetae (136)

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Parasitology (1961), **51**, 111–115
With 3 text-figures
Printed in Great Britain

On *Cercaria chungathi* Peter & Srivastava, 1955 and its relationship to *Gastrothylax crumenifer* (Creplin)

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(*Received* 8 *January* 1957)

While examining the local aquatic snails for trematode infection, Peter & Srivastava (1955) encountered a new species of amphistome cercaria which they named *Cercaria chungathi*. It was obtained from *Gyraulus convexiusculus* (Hutton). Transmission experiments conducted during the present investigations revealed it to be the larva of *Gastrothylax crumenifer* (Creplin).

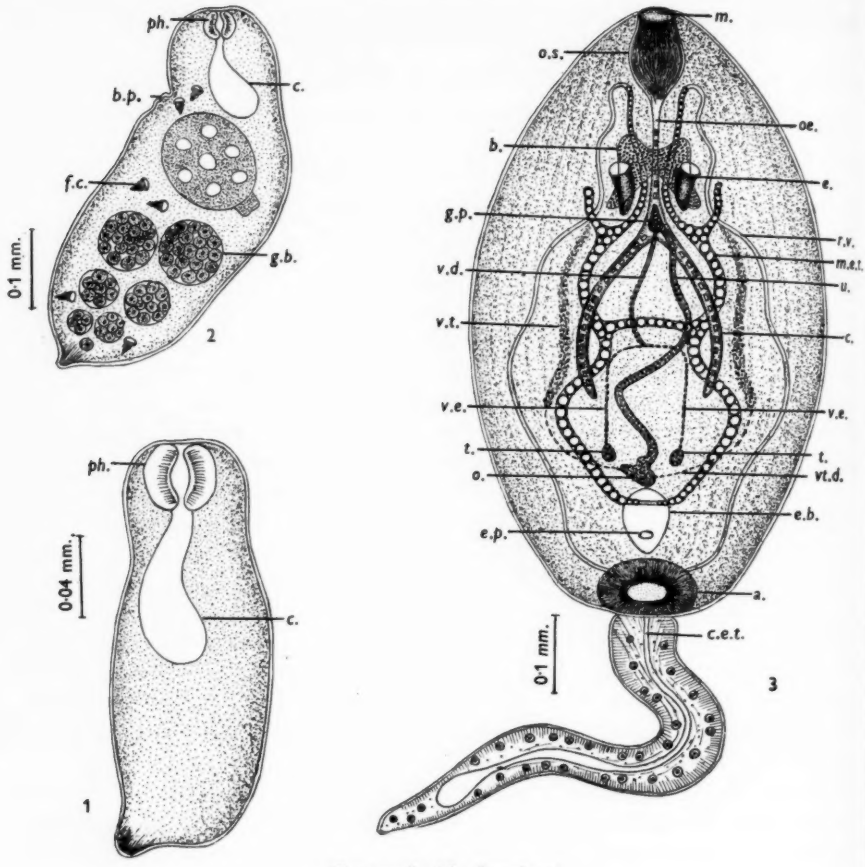
G. crumenifer is a pouched amphistome commonly occurring in the rumen of cattle, buffaloes, sheep and goats in India. Preliminary observations on the life cycle of this fluke were made by Srivastava (1944), who found that under experimental conditions very young *Indoplanorbis exustus* acted as its intermediate host. Besides proving that the parasite, which is innocuous in its adult stage, is highly pathogenic in its immature form, Srivastava (1947) noted that the eggs hatched in 6 days after incubation during the summer season, and the cercariae came out of the infected snails in about three weeks' time. The specific identity of the cercaria, the morphology of its parthenita and the development of the cercaria into the adult worm are described in this paper.

Fourteen specimens of the species *Gyraulus convexiusculus* collected, eight in October 1953 and six in November 1955 from Rithowra, Bareilly, were found infected with *Cercaria chungathi*. The snails discharged the larvae only when they were exposed to bright sunlight.

The redial parthenita in which the cercariae develop does not possess locomotor appendages and is devoid of any cuticular pigmentation. The mature rediae (Fig. 2) measure on an average 0·5 by 0·2 mm. The globular pharynx situated anteriorly has a diameter of about one-fourteenth of the length of the body and is followed by an empty gut which extends up to the end of the anterior one-fourth of body-length. Three pairs of flame cells are present. The birth-pore, through which the cercariae escape, is located on the ventral aspect of the body-wall on a level with the hinder end of the gut. In the immature specimens (Fig. 1), which measure 0·229 by 0·096 mm., the pharynx is one-sixth of the body-length and the gut extends nearly to the middle of the body.

SPECIFIC DIAGNOSIS OF *CERCARIA CHUNGATHI*

'Pigmentata' type. Diffuse pigmentation all over body cuticle. Body 0·252–0·569 by 0·149–0·275 mm., and tail 0·285–0·630 by 0·057–0·089 mm. Eye-spots conical with clear lens and close to level of caecal bifurcation. Oral sucker oval, 0·114 by



(Camera lucida drawings)

Fig. 1. Young redia of *Cercaria chungathi*.
Fig. 2. Mother redia of *C. chungathi*, containing growing cercaria inside.
Fig. 3. Mature specimen of *C. chungathi*.

ABBREVIATIONS

a.	acetabulum	*m.e.t.*	main excretory trunk
b.	brain	*o.*	ovary
b.p.	birth-pore	*oe.*	oesophagus
c.	caecum	*o.s.*	oral sucker
c.e.t.	caudal excretory tube	*ph.*	pharynx
e.	eye-spot	*r.v.*	retrograde vessel
e.b.	excretory bladder	*t.*	testis
e.p.	excretory pore	*v.d.*	vas deferens
f.c.	flame cell	*v.e.*	vas efferens
g.b.	germ ball	*vt.*	vitellaria
g.p.	genital pore	*vt.d.*	vitelline duct
m.	mouth	*u.*	uterus

0·062 mm. Acetabulum broader than long, 0·072 by 0·132 mm. Ratio between oral sucker and acetabulum 4/5, between acetabulum and body-length 1/8, and between acetabulum and body-breadth 1/4. Oesophagus one-fifth of body-length and without sphincter. Caeca arched and extended almost to middle of third quarter of body-length. Oesophagus and caeca filled with rectangular granules. Main excretory vessels with antero-lateral diverticula, and transverse vessel without any diverticulum and placed far behind caecal bifurcation. Excretory pore posterior to origin of main vessels. Genital pore on level with caecal bifurcation. Ovary far behind caecal termination. Uterus crosses from one side to other, 0·35 mm. long. Testes horizontal, 0·1 mm. apart, and placed posteriorly on level with ovary. Vas deferens half of uterine length.

In the presence of an antero-lateral diverticulum on the main excretory vessels and in the absence of any diverticulum on the cross-connecting vessel, *Cercaria chungathi* differs from all the other known members of the group except *Cercariae indicae* xxxii Sewell (1922). But the latter can be readily distinguished from it by the following features: the excretory cross-connexion runs adjacent to the caecal bifurcation, the eye-spots are located midway between the anterior end of the body and the level of caecal bifurcation, the oesophagus shows a well-developed sphincter, the oesophagus and caeca are without any contents, the uterus runs in the median line and the testes are markedly anterior to ovary and arranged tandem.

In the shape of the acetabulum, in the presence of granular contents in the oesophagus and caeca and in the position of testes and ovary which are placed far away from the caecal termination, the cercaria of *Gastrothylax crumenifer* resembles *Cercariae indicae* xxix Sewell (1922), which has been determined by Rao & Ayyar (1932) and Vaidyanathan (1941) to be the larva of *Fischoederius elongatus* (Poirier), another pouched amphistome of ruminants. The latter larva, however, possesses an excretory system of an altogether different pattern (diverticulum present on the cross-connexion and absent on the main vessels), besides such other distinguishing features as the presence of papillae on the margin of the mouth-opening, a shorter caeca and a diagonally dorso-ventral arrangement of the testes.

In having a horizontal arrangement of the testes, *Cercaria chungathi* agrees with *C. pseudodisci collinsi* Peter & Srivastava (1954) and *C. mosaica* Faust (1926). *C. pseudodisci collinsi*, being of the 'Diplocotylea' type, differs fundamentally from the one under study in the absence of any cross-connexion between the main excretory vessels and in the presence of a pair of oral pouches, and in the fact that the testes are located in the midregion of the body far anterior to the ovary. *C. mosaica* resembles the present cercaria in the disposition of the testes, but differs markedly in possessing peculiar eye-spots which exhibit a mosaic pattern, in the nature of the caeca which extend up to the level of the acetabulum, and in the position of the uterus which lies in the median line, and of the genital pore which is placed far posterior to the level of caecal bifurcation.

Faust (1926) noted in *C. mosaica* the topographic arrangement of the genital organs as found in the members of the genus *Gastrothylax* Poirier. The picture presented by the genital system in *C. chungathi*, where the testes are placed horizontally in the posterior part of the body on a level with the ovary and the

crossing of the uterus from one side to the other, is extremely suggestive of its relationship to *Gastrothylax crumenifer* (Creplin), and this has been experimentally proved to be the case during the present studies.

The cercariae discharged by the infected snails, after a short period of free-swimming existence, readily encyst on pieces of grass-blades provided for the purpose. The metacercariae, as is the case with other amphistome cysts, are dome-shaped. Freshly formed cysts on grass measured on an average 0·271 mm. in diameter.

DETERMINATION OF THE ADULT OF *CERCARIA CHUNGATHI*

A kid and a buffalo calf, both determined to be free from any previous trematode infection, were used as the experimental final hosts. The cysts of identified cercariae from naturally infected *Gyraulus convexiusculus* maintained in the laboratory formed the infective material. On 12 November 1953, 375 cysts were fed to the kid, and 325 cysts to the buffalo calf on 1 December 1955, and the animals were kept under conditions which precluded any extraneous trematode infection. From 2 months after the feeding of the metacercariae till the termination of the experiment, faecal samples from both the animals were examined on alternate days for trematode ova. Fluke eggs were first detected in the faeces of the kid on 10 March 1954, and in that of the buffalo calf on 24 March 1956, i.e. 118 days and 114 days, respectively, after infection. At autopsy, 37 flukes were collected from the kid and 34 from the buffalo calf, all from the rumen. A detailed study of the specimens proved that they were referable to *Gastrothylax crumenifer* (Creplin.)

SUMMARY

The post-cercarial development of *G. crumenifer* (Creplin) has been experimentally elucidated.

Gyraulus convexiusculus (Hutton) serves as the intermediate host under natural conditions.

The adult stage of the fluke was raised experimentally in ruminants, the time taken by the parasite to attain maturity being 118 days in the kid and 114 in the buffalo calf.

Cercaria chungathi Peter & Srivastava, 1955, has been established to be the larva of *Gastrothylax crumenifer*. The cercaria, the redial parthenita and the metacercaria have been described.

The authors are grateful to the Director, Indian Veterinary Research Institute, for his keen interest in these studies.

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Parasitology (1961), **51**, 117–122
With 10 *text-figures*
Printed in Great Britain

Studies on two new Cephaline gregarines from the intestine of Indian insects, *Gryllodes sigillatus and Liogryllus bimaculatus**

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(*Received* 8 *September* 1959)

I. INTRODUCTION

Up to the present gregarines from crickets have only been recorded outside India. They belong to two genera, *Gregarina* and *Leidyana*, occurring in three species of *Gryllus*: *G. abbreviatus*, *G. pennsylvanicus* and *G. americanus*. It is surprising that the intestinal protozoan fauna of some of the common Indian crickets have not hitherto been studied.

In the present paper a description is given of two new species of Cephaline gregarines: one, from a house cricket *Gryllodes sigillatus*, belonging to the genus *Stenophora*; the other, from the black cricket *Liogryllus bimaculatus*, belonging to the genus *Bulbocephalus*. These insects also harboured some other intestinal protozoa which will be described separately. It is remarkable that, of the seven known species of *Stenophora*, none has been recorded from insects, and only two from India. As regards the genus *Bulbocephalus*, only two species are on record, both of which were found in larvae. In the present paper the occurrence of this genus in India is reported for the first time.

II. MATERIAL AND METHODS

The house crickets were collected from dark places in the houses, where they were abundant in corners and crevices of the college hall kitchens, while some were found in my room, where the lower part of the almirah was packed with papers to provide shelter for these insects. They were collected from the same habitats at Lucknow and Jalaun, both in the United Provinces, India. The incidence of infection in house crickets was not high: out of 100 dissected by me, gregarines were found only in four, but in these the infection was heavy and in some parts of the gut the parasites were packed in clusters. The black crickets were collected from lighted places, for example, under lamp-posts on the streets and roads, while some of them were taken in the laboratory, where they were attracted by the strong illumination. More than fifty crickets were dissected by me and their intestinal contents examined, but only one of them harboured gregarines of the genus *Bulbocephalus* alone, though their number exceeded 200.

The gregarines were first examined alive in normal saline. Some of them were

* This paper forms part of a thesis accepted for the degree of Doctor of Philosophy in the University of Lucknow.

fixed on slides, others in watch-glasses, using Schaudinn's fluid, Champy's fluid, corrosive sublimate or 1 % osmium tetroxide, the first of which produced the best results. The preparations were stained with Mayer's haemalum or iron haematoxylin, which produced the best results, but acid fuchsin, thionin or aurentia (the last three being in alcoholic solution) were also used.

III. DESCRIPTION

(1) *Stenophora gryllodes-sigillatae* sp.nov.

Gregarines of the genus *Stenophora* Labbé, 1899, belonging to fam. Stenophoridae Léger & Duboscq, 1904, have solitary sporadins, with a simple epimerite or none at all; their spores are always ovoid with an equatorial line and are not arranged in chains. In 1848 this genus was included by Frantzius in *Gregarina*, then Schneider (1875) renamed it *Stenocephalus*, while in 1899 it was separated by Labbé as *Stenophora*. Up to the present it was represented by seven genera, none of which was found in insects. The gregarine described here is parasitic in the intestine of *Gryllodes sigillatus*, a house cricket collected at Badshahbagh, Lucknow and Jalaun, India.

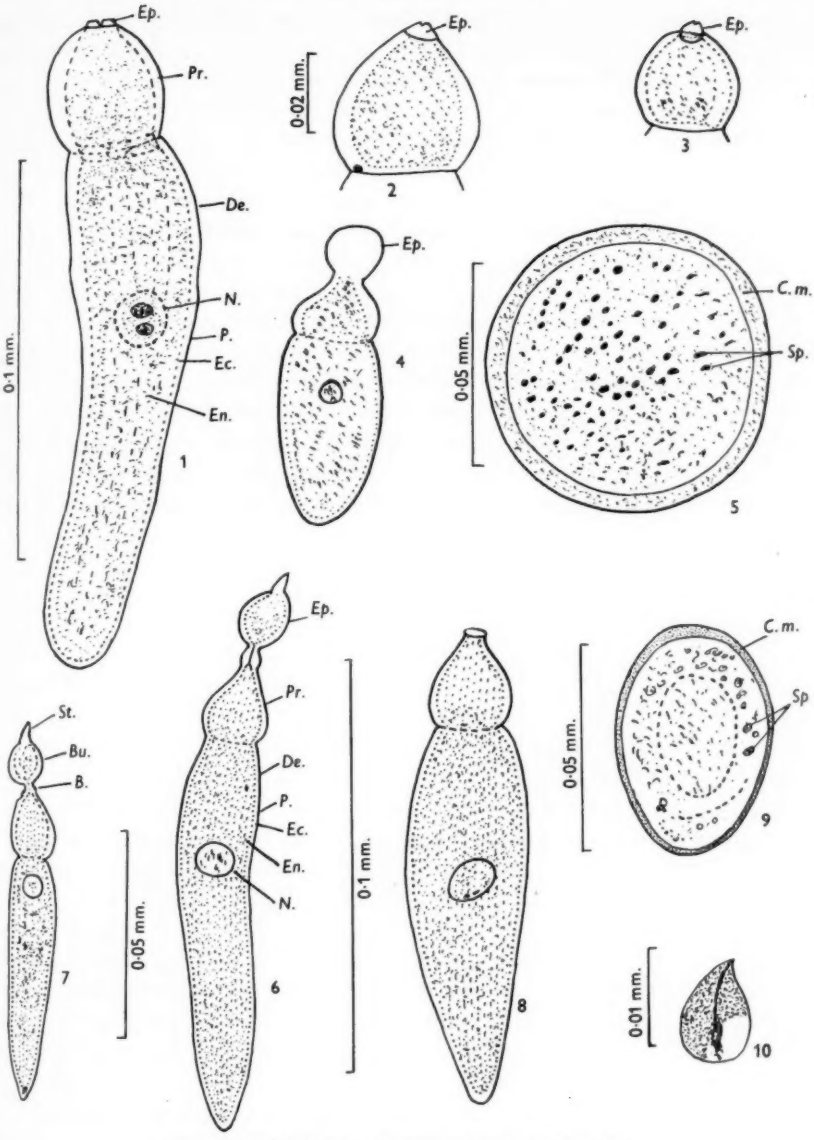
The trophozoites of this gregarine measured from 140 to 194 μ in length and from 32 to 40 μ in breadth, as shown in Table 1.

Table 1. *Measurements of* Stenophora gryllodes-sigillatae *sp. nov.* (μ)

Total length of body	Width of body	Approximate ratio of length to width of body
160	32	5·0
140	35	4·0
170	33	5·1
194	40	4·9
192	33	5·8

On examination in living condition the gregarines appear to have a somewhat yellowish tinge, which is due to stored food in the deutomerite. The body can bend during movements, but at other times remains straight; the changes in the body can be considerable, as shown by the ratio of length to width of the body, which is from 4·0 to 5·8 (average 5·0).

The trophozoites are elongated in shape (Fig. 1). The posterior part of the body is always tapering though its extremity is rounded; the widest part of the body is in the anterior quarter of the deutomerite. In young forms (Fig. 4) the epimerite is rounded and hyaline, measuring about 12–13 μ in diameter. Ray (1933) and Chakravarty (1934) noted this character in describing Indian species of the present genus. In adult forms it is either absent or is represented by an apparently bilobed, transparent, blunt, conical or rounded (with a notch present) structure (as shown in Figs. 1–3, respectively), but it is always very small. The protomerite is either dome-shaped (Fig. 1), conical at the anterior end (Fig. 2) or slightly globular (Fig. 3). Its length varies from 26 to 40 μ and its width at the widest part, which is



Stenophora gryllodes-sigillatae sp.nov. (Figs. 1–5).

Fig. 1. An entire trophozoite. Fig. 2. Protomerite with conical epimerite. Fig. 3. Protomerite with rounded epimerite. Fig. 4. Trophozoite (young form). Fig. 5. Cyst.

Bulbocephalus indicus sp.nov. (Figs. 6–10)

Fig. 6. An entire trophozoite (adult). Fig. 7. Trophozoite (young). Fig. 8. Trophozoite without epimerite, but with point of break. Fig. 9. Cyst. Fig. 10. Spore. *B.*, base; *Bu.*, bulb; *C.m.*, cyst membrane; *De.*, deutomerite; *Ec.*, ectoplasm; *En.*, endoplasm; *Ep.*, epimerite; *N.*, nucleus; *P.*, pellicle; *Pr.*, protomerite; *Sp.*, spore; *St.*, style.

generally in the posterior half, is from 26 to 36 μ, while its ratio to total body length is from 1 : 4 to 1 : 5. The posterior quarter of the protomerite stains darkly, while the rest is transparent. The ratio of the width of the protomerite to body width is nearly 1 : 1. The deutomerite forms the major part of the body. At the anterior end it is separated from the protomerite by a septum; its outer wall (i.e. pellicle) takes a darker stain, while the ectoplasm is transparent. The contents of the deutomerite stain darker; and sometimes longitudinal striations are seen on it. The nucleus measures about 10 μ in diameter; it contains two large darkly stained bodies which probably represent chromosomes. The nucleus is always situated in the anterior half of the body.

The cysts of this gregarine are rounded in shape and have no sporoduct, their membrane is only 5–7 μ in thickness, therefore the cyst is not very opaque. It contains spores and measures about 70 μ in diameter. They look oval in shape, but since their dehiscence was not seen by me I have not described them here.

The present species has been compared with all the seven known species of the genus *Stenophora*, from various hosts, and has been found to differ markedly from all of them in shape, size of the body and nature of the epimerite. The species in question and their hosts are listed below:

1. *S. diplocarpa* from *Euryurus erythropygus*
2. *S. impressa* from *Parajulus impressus*
3. *S. lactaria* from *Callipus lactarius*
4. *S. larvata* from *Spirobolus spinigerus*
5. *S. robusta* from *Parajulus venustus*, *Orthomorpha gracilis* and *Orthomorpha* sp.
6. *S. khagendrae* from a millipede
7. *S. ellipsoidi* from *Diplopoda* sp.

The gregarine from the cricket *Gryllodes sigillatus*, which is recorded for the first time from this host and from an insect in general, is regarded as a new species, for which I propose the name *Stenophora gryllodes-sigillatae* sp.nov.

(2) *Bulbocephalus indicus* sp.nov.

Gregarines of the genus *Bulbocephalus* Watson, 1916, belonging to the cephalina fam. Stylocephalidae Ellis, are characterized by an epimerite in the form of a dilated papilla, situated in the middle of the long neck. At present only two species of this genus are known: *B. wardi* from the intestine of Clerid larvae, which is the type species of the genus erected by Watson (1916), and *B. elongatus* described by her from the gut of *Cucujus* larvae. The gregarine described here was obtained from the intestine of *Liogryllus bimaculatus*, a black cricket collected at Badshahbagh, Lucknow, India.

The trophozoites of this gregarine measured from 90 to 175 μ in length and from 15 to 30 μ in breadth, as shown in Table 2.

The trophozoites are elongated and move parallel to the surface; usually the body remains straight but sometimes it is found to be bent to one side; all the forms are solitary. The presence of a bulbous epimerite is very characteristic of this form, the structure of which can be studied better in living condition. The body is transparent

and elongated; the ratio of the width to length of the body is generally 1:6, but in cases where the epimerite has been separated (Fig. 8), it is reduced to 1:4, while in very elongated forms it attains 1:8. The epimerite consists of three parts (Fig. 6): (i) a base fitting on the apex of protomerite, which has a slight swelling; (ii) a spherical bulb; and (iii) a style-like structure at the apex of the bulb of epimerite. The epimerite is 16–26 μ long, and ratio to the body length is 1:5 or 1:5·5; its contents are more transparent than those of the protomerite. The style-like structure is probably formed only by the outer layer of body ectoplasm. In the present case the base of the epimerite is much narrower than in the other two known species of the genus. The protomerite is 17–25 μ long and 12–20 μ wide. It is narrow towards the anterior end and broadest towards the posterior part, narrowing again at the level of the septum. The ratio of protomerite length to the total body length varies from 1:5 to 1:6; its contents take a dark stain. In Fig. 8 the epimerite has been broken off. The deutomerite is elongated; its broadest part is in the anterior half, while the posterior end is tapering, but rounded at the end. Over the whole of the protomerite and deutomerite some longitudinal striations are present; its contents stain slightly darker than those of the protomerite.

Table 2. *Measurements of* Bulbocephalus indicus *sp.nov.* (μ)

Total length of body	Width of body	Approximate ratio of length to width of body
90	15	6·0
121	30	4·0
135	21	6·0
118	20	6·0
175	22	8·0

The position of the nucleus is not fixed, but it is always in the anterior half of the body; sometimes it is oval and sometimes rounded in shape. Owing to the dark contents of the deutomerite, chromosome studies could not be made.

Some cysts have been found; they have a comparatively thin outer membrane and are oval in shape (Fig. 9) measuring 50–60 $\mu \times$ 30–40 μ; no sporoducts have been seen. On the slide one cyst has been found in ruptured condition, from which many spores with one end rounded and the other pointed have emerged (Fig. 10); they measure 7–8 $\times$ 5–6 μ. Some spores also look slightly rounded; actual dehiscence has not been observed.

The present species has been compared with the only two known ones, i.e. *Bulbocephalus wardi* and *B. elongatus*. Although it bears some resemblance to *B. wardi* Watson in length of the body, it differs from it in lesser width of the body, in the base of the epimerite, which is altogether different in the new gregarine, in a shorter neck, and in possessing striations all over the body. The same characters distinguish the present species from *B. elongatus* which is very much elongated. On the basis of these differences, a new species, *Bulbocephalus indicus* sp.nov., is erected for this form. This is the first record for the genus from India, and it raises the number of its species to three.

SUMMARY

A description is given of two new Cephaline gregarines from Indian crickets collected at Lucknow and Jalaun, United Provinces.

One of these, *Stenophora gryllodes-sigillatae* sp.nov., from the gut of *Gryllodes sigillatus*, has solitary slender trophozoites up to 194 μ long. Its epimerite is rounded in young forms and absent or represented by its remnant in adults. The nucleus has two chromosomes. Cysts are rounded, invested in a very thin membrane and without sporoducts.

The second, *Bulbocephalus indicus* sp.nov., from the gut of *Liogryllus bimaculatus*, is characterized by solitary elongated sporadins; the neck is short and a bulbous epimerite is always present. The body, measuring up to 175 μ in length and up to 30 μ in breadth, presents a striated appearance. Cysts are oval, covered by a very thin membrane, and have no sporoducts.

The author is very grateful to Dr S. M. Das, under whose able guidance this work was carried out. His thanks are also due to the Department of Zoology, University of Lucknow, for providing the laboratory facilities.

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Parasitology (1961), **51**, 123–126
With 1 text-figure
Printed in Great Britain

On a new trematode *Echinoparyphium bagulai* sp.nov., (Echinostomatidae) from *Anas poecilorhyncha*

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(*Received* 26 *October* 1959)

INTRODUCTION

In November 1953, about one-half per cent of *Lymnaea luteola* taken from a pond in Alfred Park, Allahabad, were infected with an echinostome cercaria. The first collections of these cercariae were made by Dr Onkar Nath Srivastava, who was surveying cercarial infections in the snails and who kindly gave me the echinostome material. Additional material was obtained by numerous subsequent collections. After the cercaria was described it was possible to undertake a limited number of experiments in an attempt to discover other stages of the life cycle. It was found that *Lymnaea luteola* is both the first and the second intermediate host of a new species of *Echninoparyphium*. The adult of this new species, for which the name *E. bagulai* is proposed, matures in the intestine of the domestic duck, *Anas poecilorhyncha*. When this duck was experimentally infected with cercariae, the adult trematode was recovered from the intestine of this duck 21 days after its infection.

The present paper deals with the morphology of the new species, *E. bagulai* The results of a study of other stages in the life cycle will be published in subsequent papers.

THE ADULT (Figs. 1, 2)

Description. The following description is based on sections and whole preparations of about fifty mature specimens taken from *Anas poecilorhyncha*. Mature worms small and elongate, size 1·568 by 0·88 mm. to 2·88 by 0·896 mm. Widest level usually at the acetabulum. Cuticular spines relatively large, extending dorsally to the acetabulum. Oral sucker small, terminal. Head collar with double, dorsally-uninterrupted crown of forty-two spines; corner spines definitely larger than marginal spines. Prepharynx short 0·0352 mm.; pharynx ovoid, length 0·066 by 0·0528 mm. Oesophagus relatively long, bifurcating just in front of acetabulum. Intestinal caeca regular, extending to the posterior end of the body. Acetabulum some distance in front of the middle of the body, somewhat spherical, with thick walls and a diameter about 0·365 by 0·321 mm. Testes tandem, elongate, with simple margins, the anterior testis typically wider than the posterior one. Their location varies with length of worm, but they tend to lie in the posterior half of the body. Cirrus sac small, pyriform, dorsal to the acetabulum, with a diameter of 0·228 mm. Cirrus sac nearly filled by the seminal vesicle; cirrus simple and very

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long. Genital pore between the acetabulum and the bifurcation of the gut. Ovary in the median line, anterior to the testes, oval in outline, with a diameter of 0·127–0·154 mm. Oviduct leading to the ootype and surrounded by a well-developed shell gland. Vitelline follicles extending from the posterior level of the

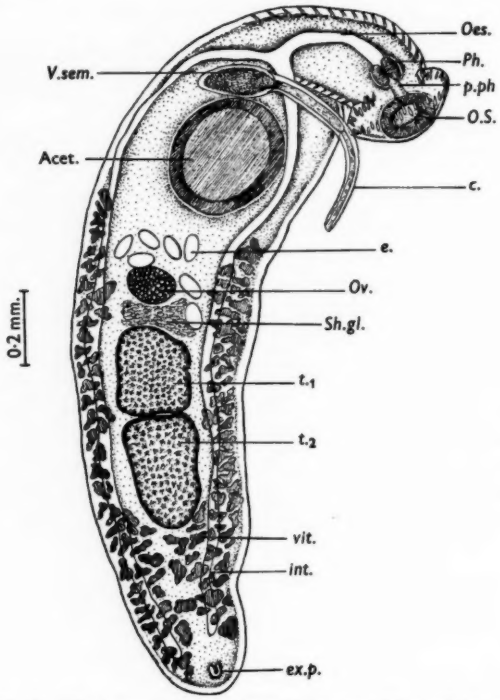

Fig. 1. *Echinoparyphium bagulai* sp.nov. Ventral view.

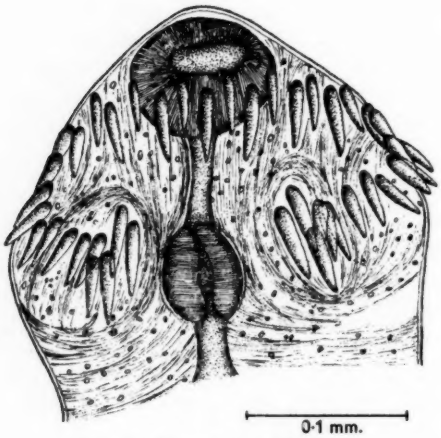

Fig. 2. Head crown of adult.

acetabulum to the posterior end of the body and confluent in the post testicular space. Loops of the uterus few, mostly transverse, and intercaecal. Eggs few, oval, measuring 0·0528–0·0792 by 0·044–0·0484 mm.

DISCUSSION

Dietz (1909) gave a historical review of the family *Echinostomatidae* (Poche, 1925) and created several genera, including *Echinoparyphium*, naming *E. elegans* (Looss, 1899) as the type species. He gave, as the diagnostic features of the genus, the presence of double rows of collar spines of different sizes and vitelline follicles commencing far below the level of the acetabulum (mostly at the posterior ends of the testes) and not meeting in the median line behind the testes. Dollfus (1951) described a new species, *E. baculoides*, which had vitelline follicles commencing at the posterior margin of acetabulum and extending up to the posterior end of the body, to meet in the post testicular region.

The features of the collar spines and vitelline follicles just given place *E. bagulai*, the species here described, in the genus *Echinoparyphium* (Dietz).

Dollfus (1953) reviewed the genus and listed the known species. Since then the following species have been added: *E. petrowi* by Nevostrueva (1953); *E. paracinctum* and species *innom* by Bychovskaya-Pavlovskaya (1953). Dollfus did not include the species *E. ellisi* Johnston & Angel (1949); *E. jubilarum* Elperin (1937) and *E. microvitellatum* Oschmarin (1947) in his list. There are twenty-eight more or less well-known species which have been placed in the genus *Echinoparyphium* by Yamaguti, (1958). He removed the species *E. petrowi* and placed it as the genotype of his new genus, *Neoacanthoparyphium*, because the vitellaria form on each side a longitudinal row of several large compact clusters of follicles.

The numerous species of the genus *Echinoparyphium* are based on the number of collar spines and especially on the arrangement and unequal size of the collar spines. These are the most reliable characters for the differential diagnosis of closely allied species. Mendheim (1943), Dollfus (1953), Yamaguti (1958) and many others seem to hold the same opinion. On the other hand, some have argued, notably Dollfus (1953), that the character of the vitellaria is too variable and should not be given specific significance.

As a result of the present study the following characters have been adopted as of diagnostic value: the number of the collar spines; the relative sizes of the various spines; the presence of dorsal cuticular spines; the small cirrus pouch dorsal to the acetabulum; the rounded or slightly elongated gonads and the length of the uterus.

In studying the descriptions of closely allied forms, the above characteristics have been used as a basis for conclusions regarding relationship. Other characteristics, such as the size of the body and the eggs have also been noted. *E. bagulai* sp. nov. is distinguished from other species by having forty-two cephalic spines, but it closely resembles *E. baculoides* (Dollfus) in almost all features, except the number of collar spines.

The author wishes to express most sincere thanks and gratitude to Professor H. R. Mehra for his suggestions and assistance during the progress of this work.

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EXPLANATION OF FIGURES

Fig. 1 was made with the help of a camera-lucida and details were filled in at the same magnification.

Abbreviations used

Acet., acetabulum; *c*, cirrus; *e*, eggs; *exp.p.*, excretory pore; *int.*, intestine; *Oes.*, oesophagus; *O.S.*, oral sucker; *Ov.*, ovary; *Ph.*, pharynx; *p.ph.*, prepharynx; *Sh.gl.*, shell gland; *t.*, testes; *V.sem.*, vesicula seminalis; *vit.*, vitelline follicles.

Parasitology (1961), **51**, 127–132
With 5 text-figures
Printed in Great Britain

Studies on the excretory system of amphistome parasites of ruminants

II. The genera *Gastrothylax* Poirier, 1883, and *Fischoederius* Stiles & Goldberger, 1910

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(*Received* 1 *February* 1960)

INTRODUCTION

The amphistomes are most commonly parasitic in ruminants throughout the world. Large numbers of them may be present in a single host and they provide good material for all kinds of studies. This paper is in continuation of a series of studies on the morphology and life histories of these worms.

Many helminthologists have emphasized the importance of the excretory system as a means of classifying trematodes. A history of earlier work on the excretory systems of trematodes was given by the author (Tandon, 1958*a*) in his paper on the excretory system of *Carmyerius spatiosus* (Stiles & Goldberger, 1910) and Tandon (1957, 1958*b*) described this system in the larval forms of *Gastrothylax crumenifer* and *Fischoederius elongatus*. The present paper deals with the excretory systems of three species of the two genera *Gastrothylax* Poirier, 1883 and *Fischoederius* Stiles & Goldberger, 1910, which belong to the subfamily Gastrothylacinae Stiles & Goldberger, 1910.

MATERIALS AND METHODS

The worms were obtained from local slaughterhouses in which sheep (*Ovis aries*), goats (*Capra indica*), and buffaloes (*Bos bubalis*) are regularly slaughtered for human consumption. Worms of all sizes and ages are available throughout the year. Some specimens of *Gastrothylax crumenifer* were also obtained from an experimental infection of a goat-kid. The methods used were those described in a previous paper (Tandon, 1958*a*).

I. *GASTROTHYLAX CRUMENIFER* (CREPLIN, 1847)

The excretory system (Fig. 1) has the H-shaped pattern characteristic of amphistomes, the horizontal bar of the letter H being almost at the middle of the body of the worm. The anterior arms of the H are forked, while the posterior ones join in the middle line below the excretory bladder. The excretory pore opens dorsally at the posterior end of the body, immediately in front of the acetabulum and behind the opening of the Laurer's canal. The excretory bladder is large; it has either an oval or an elongate oval, outline and it lies parallel to, and near, the

acetabulum and may even touch the latter. The excretory pore is postero-median on the excretory bladder.

The two main longitudinal excretory ducts (Fig. 1, *l.e.d.*) open on the ventral surface of the excretory bladder and run laterally forwards, almost internal to the intestinal caeca; they terminate anteriorly near the middle of the oral sucker.

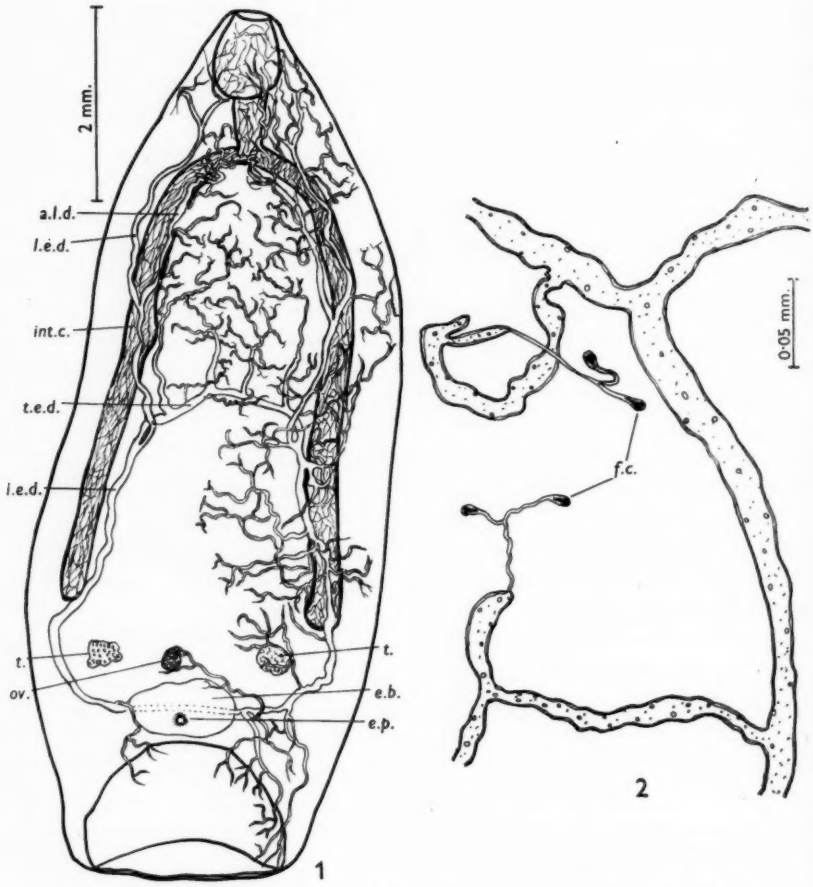

Fig. 1. The excretory system of *Gastrothylax crumenifer* from dorsal side.
Fig. 2. Flame cells at the end of the excretory tubules in the same.

The anterior portion of each main longitudinal excretory duct (Figs. 1, 3, 5, *l.e.d.*) is Y-shaped, because each receives internally, behind the bifurcation of the intestine, an antero-lateral branch (Figs. 1, 5, *a.l.d.*) from the anterior part of the body. Each main longitudinal excretory duct also receives secondary lateral and longitudinal branches from various parts of the body. Among these, the branches from the ventral pouch, which are usually prominent in members of this sub-

family, run, in this species, ventro-laterally to end by forming the main longitudinal excretory ducts on their ventral side.

The transverse excretory duct (Fig. 1, *t.e.d.*) usually receives four branches, from the anterior ends of the intestinal caeca and the region behind this and from the terminal portions of the reproductive ducts.

The capillary excretory tubules form a network around the intestinal caeca, the reproductive organs, the ventral pouch and the acetabulum and they also collect fluid from the body wall. Counting the main longitudinal excretory duct as the primary one, the branches that are the finest are of the fifth order.

The excretory products are collected, by the action of the flame cells, from the various parts of the body, into the capillary tubules, which deliver them into larger and larger ducts, until they reach the main longitudinal excretory ducts and finally the excretory bladder. The flame cells were seen at the ends of the finest capillary tubules. In this species two flame cells (Fig. 2, *f.c.*) were present, at the end of the last branch, which received two capillaries from the two cells. Each flame cell was 0·013 mm. long. The excretory ducts were found full of a colourless fluid, in which small, rounded, shining bodies were dispersed.

II. *FISCHOEDERIUS ELONGATUS* (STILES & GOLDBERGER, 1910)

The excretory system in this species (Figs. 3, 4), though it shows the common amphistome pattern, presents certain variations, due probably to the elongated and narrow body of this species and its short intestinal caeca. The excretory pore opens posterodorsally, behind the opening of the Laurer's canal and a little distance away from the acetabulum. The excretory bladder is large and oval and is placed in front of the acetabulum.

The transverse excretory duct (Fig. 3, *t.e.d.*) of this species is very small. The two longitudinal excretory ducts (Fig. 3, *l.e.d.*) begin near the middle of the oral sucker and run external to the intestinal caeca throughout their length, except for a short distance at the level of the transverse excretory duct. This latter part of their course differs from that of the corresponding ducts of *G. crumenifer*. Thus each longitudinal duct curves inwards, at about the junction of the anterior and middle thirds of the body, to join the very small transverse excretory duct (Fig. 3, *t.e.d.*). Each longitudinal excretory duct joins the transverse excretory duct at the junction of the middle and posterior thirds of the intestinal caeca, which reach only up to the middle of the body in this species. The two longitudinal excretory canals end by opening into the ventro-lateral aspect of the excretory bladder.

The transverse excretory duct, however, receives, at the middle of its length, a branch which runs forward for a short distance and then divides into two branches which reach up to the intestinal bifurcation, so that a more or less Y-shaped median longitudinal excretory duct (Fig. 3 ,*m.l.d.*) is formed; and this receives smaller branches from the anterior region of the body.

A large number of branches and subbranches are received by the main longitudinal excretory ducts; these come, as they do in the other species, from the intestinal caeca, reproductive organs, ventral pouch, body wall and suckers. The

anterior portions (*a.l.d.*) of the main longitudinal excretory ducts are not, in this species, bifurcated, as they are in *G. crumenifer*, although smaller branches enter them near their terminations. The main ducts are connected, as they are in *G. crumenifer*, through the sub-branches up to the fifth series, which terminate in

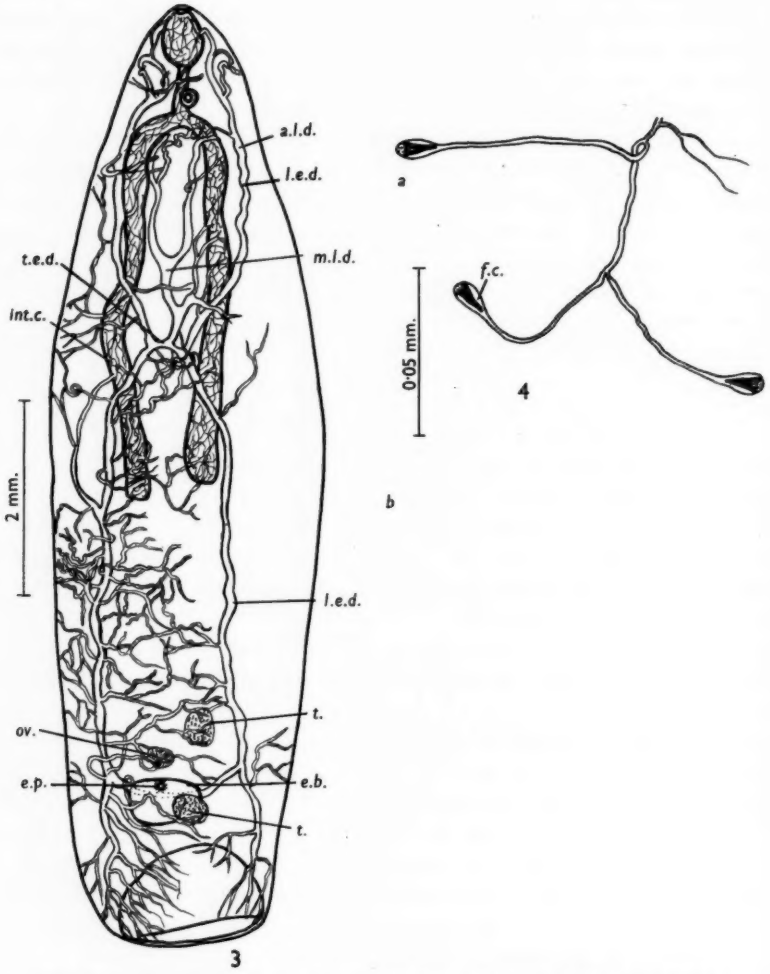

Fig. 3. The excretory system of *Fischoederius elongatus* from dorsal side.
Fig. 4. Flame cells at the end of the excretory tubules in the same.

flame cells. Each of the finest capillaries of the fifth series receives at its end three tubules from the three flame cells (Fig. 4). The flame cell is on an average 0·01 mm. long. The excretory ducts of the living worm are filled with a transparent fluid in which there are large shining bodies; and the larger ducts can be seen contracting and expanding alternately.

III. *FISCHOEDERIUS COBBOLDI* (STILES & GOLDBERGER, 1910)

The excretory system in this species (Fig. 5) although it shows the common amphistome pattern, is intermediate between that of *G. crumenifer* and that of *F. elongatus*. The excretory pore in this species also opens postero-dorsally, immediately in front of the acetabulum and behind the opening of the Laurer's canal. The oval excretory bladder is generally placed parallel to the acetabulum and may

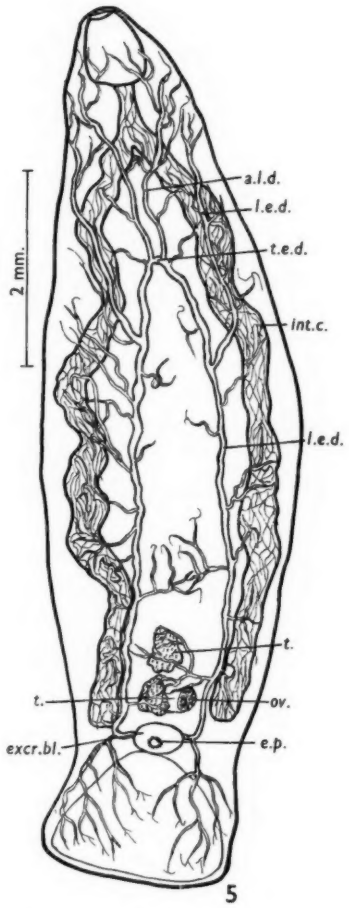

Fig. 5. The excretory system of *Fischoederius cobboldi* from the dorsal side.

sometimes overlap the latter. The two longitudinal excretory ducts, which open ventro-laterally into the excretory bladder, begin near the oral sucker and run down the body, internal to the intestinal caeca, as they do in *G. crumenifer*. During its course each longitudinal excretory duct receives, internally at a point about a third or halfway down the body from its anterior end, the small transverse

excretory duct, as it does in *F. elongatus*, and this duct unites it with the longitudinal duct of the other side.

The transverse excretory duct receives, from near the level of the oral sucker, two large ducts which receive branches from the intestinal caeca, oesophagus and the oral sucker. Other branches enter the longitudinal excretory ducts from the intestinal caeca, around which the capillaries form a network, and from the reproductive organs and from almost all the parts of the body, including the ventral pouch.

Each longitudinal excretory duct, before it opens into the excretory bladder, receives a large duct from the acetabulum, which is surrounded by a large number of tubules, and also a number of branches from the posterior part of the body. The branching in this species is similar to that found in *F. elongatus*.

SUMMARY

The excretory systems of *Gastrothylax crumenifer*, *Fischoederius elongatus* and *F. cobboldi* have been described. In all three species it shows the characteristic, more or less H-shaped, pattern of the amphistome excretory system.

The difference between the systems in the three species lies in the nature of the branches of the anterior portions of the longitudinal excretory ducts, in the transverse excretory ducts and the branches received by them and in the number of flame cells at the ends of the capillaries.

The main longitudinal excretory ducts run internal to the intestinal caeca in *G. crumenifer* and *F. cobboldi*, while in *F. elongatus* they run almost external to the caeca and maintain this position even in the posterior half of the body, where the caeca are not present.

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LETTERINGS IN THE FIGURES

a.l.d.	anterior portion of the main longitudinal excretory duct	*l.e.d.*	main longitudinal excretory duct
e.b.	excretory bladder	*m.l.d.*	median longitudinal excretory duct
e.p.	excretory pore	*ov.*	ovary
f.c.	flame cell	*t.*	testis
int.c.	intestinal caeca	*t.e.d.*	transverse excretory duct

Parasitology (1961), **51**, 133–172
With 31 text-figures
Printed in Great Britain

Observations on the Morphology and Life Cycle of *Neodiplostomum intermedium* (Trematoda: Diplostomatidae)

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(*Received* 25 *January* 1960)

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I. INTRODUCTION

The adult stage of *Neodiplostomum intermedium* was found first in the allied rat, *Rattus assimilis* Gould, by Pearson (1959*b*) and has since been found in the water rat, *Hydromys chrysogaster* Geoffroy. This study of the life cycle began with the finding of lappet-less diplostomula in a frog (*Hyla pearsoni* Copland*), which developed into *Neodiplostomum intermedium* when fed to laboratory rats and laboratory-reared allied rats. Using eggs from the faeces of experimentally infected rats, the two species of snails suspected of being the first intermediate host were exposed. One of the species, *Pettancylus assimilis* (Petterd), became infected and released cercariae, which developed into diplostomula in tadpoles of *Hyla* sp., thus completing the life cycle.

Observations on the life cycles of species of *Neodiplostomum* have been made by several workers. Cuckler (1940) reported briefly on the life cycle of *N. craterum*; this report was based on a fuller study in an unpublished Ph.D. Thesis (1941, summary 1949). Hoffman (1955) repeated the life cycle of *N. craterum*, but did not describe the various stages and Ulmer (1955) has given additional observations on this species. Turner (1958) repeated the life cycle, but as yet only a brief abstract has been published. Chandler (1942) described the complete life cycle and the various stages of *N. texensis*, a species which he considered distinct from *N. craterum*, but which Ulmer (1955) thought might not be specifically different. Leigh (1954) described briefly observations on the life cycle of a species which he said closely resembles *N. texensis*. Hoffman (1958) recorded that *Cercaria kappa* Brooks, 1948 from *Physa sayii* Tappan penetrated tadpoles and developed into a diplostomulum closely resembling that of *N. texensis* described by Chandler (1942). Penner (1938) reported that diplostomula from Florida frogs developed into a species of *Neodiplostomum* in laboratory rats, but did not describe adult or diplostomulum. Pearson (1960) has briefly described the life cycle of *N. buteonis*.

II. MATERIALS AND METHODS

Rats were infected by feeding them whole infected tadpoles. Living larval stages were examined in a thick solution of methyl cellulose. To demonstrate epidermal plates, miracidia were fixed in silver nitrate by the method of Lynch (1933). Head-on and tail-on views of miracidia were prepared by Anderson's (1958) method. Cercariae were fixed with an aliquot of boiling 10% formalin and cleared in glycerine for measuring. Diplostomula and adults were fixed by pipetting into boiling 5% formalin.

To follow the early development of the miracidium in individual eggs, washed eggs from faeces were mounted in a thin film of water on a coverslip and sealed to a depression slide with vaseline. Eggs in such sealed preparations developed and hatched in the same manner as eggs in ordinary cultures.

Tadpoles of *Hyla* sp. were reared in the laboratory from egg masses collected in the field and fed on boiled lettuce and commercial fish food. The tadpoles were

* Described since this paper was submitted. Throughout text for '*Hyla* sp.' read '*Hyla pearsoni*'.

identified by rearing them to the stage of young frogs and comparing these with adult frogs collected from the same stream. Tadpoles were identified as belonging to *Hyla latopalmata* (Günther) and *Mixophyes fasciolatus* Günther by comparing the frogs into which they metamorphosed with identified adult frogs from the same area.

III. THE LIFE CYCLE

(*a*) *First intermediate host*

Two species of snails, a pulmonate limpet, *Pettancylus assimilis* (Petterd), and a prosobranch, *Posticobia brazieri* (Smith), were found in the same stream as tadpoles naturally infected with diplostomula. When laboratory-reared juveniles of these two species were exposed to miracidia, many of the limpets, but none of the prosobranchs, became infected. At summer temperatures (range 22·8–29·4° C.) cercariae first emerged 19 days after exposure. Unfortunately none of the laboratory-reared limpets survived beyond the first few days of cercarial emergence and to obtain enough cercariae for both morphological study and the exposure of tadpoles, it was necessary to use wild limpets from a local temporary pond as hosts. To avoid possible confusion with natural infections, wild limpets were examined under a dissecting microscope in a horizontal beam of light, a method found effectual in locating young mother sporocysts *in situ* in laboratory-reared limpets. Following exposure to miracidia, wild limpets were examined at intervals, either alive or by dissection, until cercariae emerged. The cercariae from experimentally infected wild limpets were identical with those from experimentally infected laboratory-reared limpets; furthermore, these cercariae developed in tadpoles into diplostomula, which, in turn, developed into *Neodiplostomum intermedium* in rats. Hence, it is considered that all stages described herein belong to *N. intermedium*.

(*b*) *Second intermediate host*

Tadpoles and frogs of *Hyla* sp. were shown to be natural hosts by feeding diplostomula from them to *Rattus assimilis* and laboratory rats and recovering adults of *Neodiplostomum intermedium* at autopsy. Laboratory-reared tadpoles of *Hyla* sp. were infected experimentally, development of the metacercaria taking about 2 weeks (temperature range 22–31° C.), and fed to *Rattus assimilis*, from which adult worms were subsequently recovered.

Diplostomula, indistinguishable from those from experimentally infected tadpoles, were found in tadpoles of *Hyla latopalmata* (Günther), in adults of an unidentified leptodactylid, and in tadpoles of *Mixophyes fasciolatus* Günther. Examination of frogs and tadpoles from two streams in the same area revealed that whereas 110 of 161 tadpoles and frogs of *Hyla* sp. were infected with diplostomula, only one of thirty-two frogs of the leptodactylid, and one of 102 tadpoles of *Mixophyes fasciolatus* were infected with a single diplostomulum each. These figures suggest that *Neodiplostomum intermedium* shows specificity in its choice of second intermediate host, preferring *Hyla* sp. (Fam. Hylidae) to the leptodactylid and to *Mixophyes fasciolatus* (Fam. Leptodactylidae).

(*c*) *Paratenic, or transport, hosts*

Twenty diplostomula from experimentally infected *Hyla* sp. were fed by mouth to a young laboratory-reared tree frog, *Hyla caerulea* (Shaw). Three days later two diplostomula were found free in the body cavity. Small numbers of diplostomula *in situ* in naturally infected tadpoles were fed to two pink-tongued skinks, *Hemisphaerodon gerrardi* Peters, born in the laboratory, and two bearded dragon lizards, *Amphibolurus barbatus* Cuvier, hatched in the laboratory. At autopsy, one pink-tongued lizard contained three diplostomula 25 days after infection. No diplostomula were found in the second pink-tongued lizard at 3 days, or the two bearded dragons at 34 and 53 days after infection.

It appears, then, that lizards, and probably frogs, can serve as paratenic hosts for the diplostomulum. The ability of larval stages (both diplostomula and mesocercariae) to survive in various non-definitive hosts is common to a number of mammalian diplostomatids, as has been shown for *Neodiplostomum craterum* by Cuckler (1940; 1949) and Turner (1958), *N. texensis* by Chandler (1942), *N. buteonis* by Pearson (1960), *Pharyngostomum cordatum* by Wallace (1939), and for *Alaria* spp. (summary in Pearson, 1956).

(*d*) *Definitive host*

Neodiplostomum intermedium was first found in *Rattus assimilis* Gould by Pearson (1959*b*) and has since been found in the water rat, *Hydromys chrysogaster* Geoffroy.

When diplostomula were fed to *Rattus assimilis* and laboratory rats, eggs first appeared in the faeces 7 or 8 days later. One *R. assimilis* continued to pass eggs in large numbers for 1 year after infection, whereas of three laboratory rats none passed eggs for more than 3 months. This difference in egg-laying period suggests that the laboratory rat is a less suitable host than *R. assimilis*.

Diplostomula were fed to three newly hatched, unfed chicks. One chick was negative on examination at 10 days, one contained a single immature adult fluke at 3 days, and the third a gravid adult at 14 days. While scanty, these results demonstrate that *Neodiplostomum intermedium* can develop to sexual maturity in unfed chicks, but whether it can develop in older birds and whether birds are important in the natural life cycle are not known.

The second question has been investigated by Ulmer (1955) who, on finding that *N. craterum* could mature in day-old chicks and noting that Leigh (1954) got *N. texensis* to mature in day-old chicks, questioned the view of Dubois & Rausch (1950) that the genus *Fibricola* can, in part, be defined by its adaptation to mammals. If, however, as Dubois (1944) and Pearson (1959*b*) have suggested, *Fibricola*, with species in mammals, is derived from *Neodiplostomum*, with species in birds, then it would not be surprising if species of *Fibricola* could occasionally mature in birds. I do not feel that such cross-infections invalidate the concept of the genus *Fibricola* given by Dubois & Rausch (1950) and supported, as the concept of the subgenus *Fibricola*, by Pearson (1959*b*), especially when it is recalled that only unfed day-old chicks were infected successfully.

IV. MIRACIDIUM

(*a*) *Early development*

Eggs freshly passed in faeces varied from transparent pale gold to a more opaque horn colour; they were operculate and asymmetric, and contained a zygote, with two pronuclei, lying near the opercular end surrounded by vitelline cells (Fig. 1). Thirty eggs from freshly passed faeces measured 93·0 (85·0–104·0) × 53·8 (51·8–56·4) μ.

Eggs developed rapidly at room temperature (range 18·3–26·6° C.) and began to hatch in 10–12 days. Eggs held at 5° C. were completely arrested, but developed normally when brought to room temperature as much as 3 months later.

Shortly after eggs from freshly passed faeces were first examined, the first division took place (Fig. 2*a*). The two pronuclei disappeared, presumably then fusing, and the zygote divided, usually at right angles to the longitudinal axis of the shell, into a larger cell with clear, non-granular nucleoplasm, the ectodermal or somatic cell of authors (here called E cell) and a smaller cell (here called P cell) with slightly granular nucleoplasm, the propagatory cell of authors (Fig. 2*b*). In the resting stage between divisions the nucleus with its large nucleolus reappeared in each cell. The resting stage lasted 2 hr. or more and division, from disappearance of the nucleus to appearance of nuclei in division products, took 30–40 min.

In the second division (Fig. 2*c*) the larger E cell divided into two cells similar to each other and to the parent cell. The axis of this division was at right angles and slightly oblique to the axis of the first division, so that the P cell was not in the same plane as the two E cells (Fig. 2*d*). In the third division (Fig. 2*e*), the P cell divided unequally into a larger cell like the parent cell (P cell) and a smaller cell with more granular nucleoplasm (P_1 cell). The axis of this division was at right angles to the axes of both first and second divisions, with the result that the P_1 cell lay peripherally with respect to the P cell, or obliquely adjacent to the E cells (Fig. 2*f*).

The fourth and fifth divisions occurred simultaneously in the two E cells (Fig. 2*g*), resulting in a flat quartet of E cells (Fig. 2*h*). The axes of these divisions were parallel and in the same plane, at right angles to both first and second division axes and parallel to the third division axis.

In the sixth division (Fig. 2*i*), the P cell divided for the second time, again unequally, into a larger P cell and a smaller P_1 cell, along an axis slightly oblique to that of the third cleavage (Fig. 2*j*).

In the first six divisions, which took about 2 days, there was a definite order in which the cells divided and a fairly fixed arrangement of the axes of division. In subsequent divisions, which became increasingly difficult to follow in living eggs, both order of divisions and arrangement of axes became more variable. But in the next few divisions the same pattern was followed as before, that is, E cells divided equally into E cells and the P cell divided unequally into a larger P cell and a smaller P_1 cell. When dividing, the P cell was fixed and the P_1 cell was extruded. Gradually the single P cell became surrounded by a mixture of E cells and P_1 cells.

At about the twelve-celled stage, a peripherally placed cell of P_1 type actively

squeezed between the vitelline cells, separated itself from the embryo and flattened itself against the inner surface of the shell to begin the formation of the vitelline membrane (Fig. 3*a–d*). This migration of the first cell of the vitelline membrane took about 6 hr. Once this cell had flattened itself against the shell, it could not

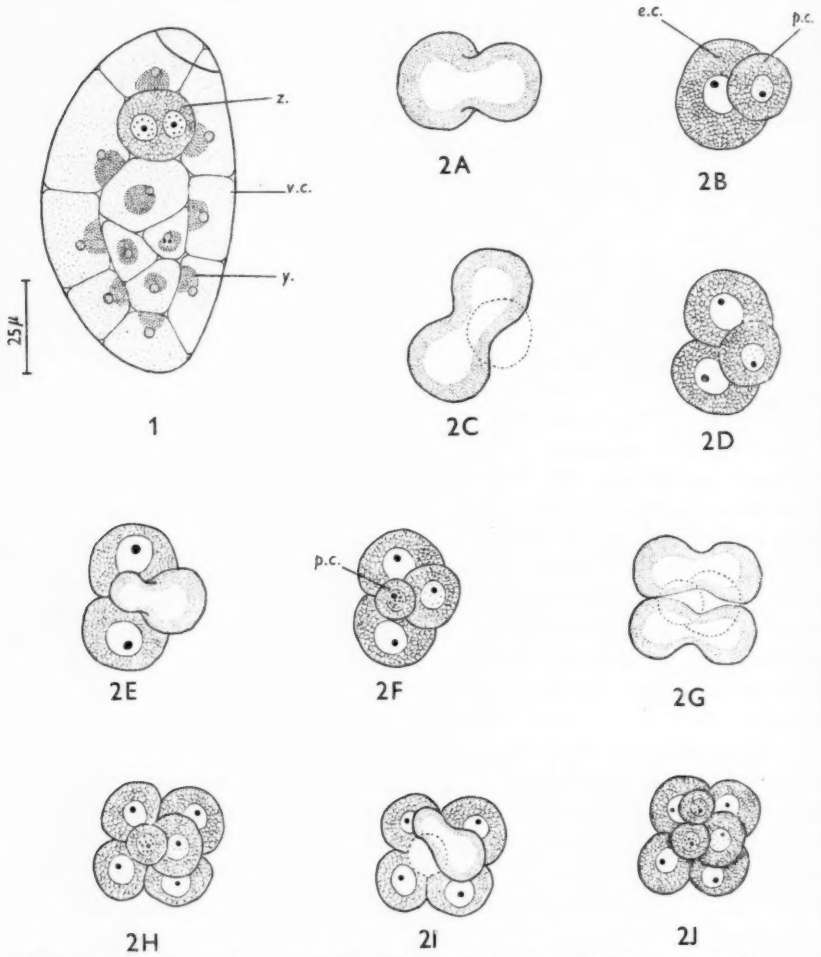

Fig. 1. Freshly passed egg, optical section, showing zygote with two pronuclei.

Fig. 2. Early cleavage of egg. (Long axis of egg parallel to long axis of page.) A, first division; B, two-celled stage; C, second division, affecting E cell (P cell shown as dotted outline); D, three-celled stage; E, third division, affecting P cell; F, four-celled stage; G, fourth and fifth divisions, simultaneously affecting two E cells; H, six-celled stage; I, sixth division, affecting P cell; J, seven-celled stage.

be seen clearly and so its subsequent development could not be followed. Indeed, the vitelline membrane was not seen clearly until miracidia were well developed. Although only a single cell of P_1 type was seen migrating to the shell in any one

egg, it was not possible to determine whether the vitelline membrane arose from a single cell or from several separate cells, because of the strong curvature of the shell and the opacity of the contents. It was, however, possible to determine that the vitelline membrane does not form from a strand or plate of cells growing out from the embryo, but from separate cells.

In a few developing eggs, some of the resting nuclei appeared to be double. For example, in one egg following the first cleavage, both E cell and P cell had two nucleoli surrounded by distinct membranes (Fig. 4). In one four-celled embryo, both *E* cells had double nuclei, whereas the P and P_1 cells had single nuclei. During later divisions the double nuclei in such cells disappeared and only single nuclei were seen. These occasional double nuclei in early blastomeres may be the result of gonomery, i.e. the separation during early divisions of the maternal and paternal chromosomes.

As the embryo grew larger, at the expense of the vitelline cells which lost their nuclei and yolk granules, it shifted from the opercular end to the middle of the egg. When the embryo had begun to elongate, the epidermal plates appeared as widely separated plano-convex swellings, with nuclei of the E-cell type and an outer covering of short motionless cilia. At this stage a few pigment granules marked the developing eyespots and the four hyaline cells could be seen posteriorly preceded by one or two germinal cells (P cells). Shortly after this the following changes were observed: the bulging epidermal plates became flattened, but retained their nuclei; the four hyaline cells grew larger, with the anterior pair enclosing a group of germinal cells; the four flame cells became feebly active; weak body contractions began to occur; the apical gland and posterior granular body appeared clearly, eyespots became darker and larger, and cilia became active; at this stage the miracidium was nearly ready to hatch. As this terminal development proceeded, the vitelline cells were reduced in size and number (partly, it appeared, by fusion) so that when the miracidium was ready to hatch there were usually two small vitelline remnants, the so-called oily masses.

The above observations on the development of the miracidium, while incomplete, show interesting differences when compared with the accounts of the development of the miracidia of *Fasciolopsis buski* by Ishii (1934), *Paragonimus kellicotti* by Chen (1937), *Parorchis acanthus* by Rees (1940) and *Megalodiscus temperatus* by van der Woude (1954). For example, whereas the first cleavage in *Neodiplostomum intermedium* into P cell and E cell was the same as that found by these four authors, the subsequent behaviour of the P cell differed. In *N. intermedium*, the P cell divided repeatedly into P and P_1 cells, while the E cell divided into similar E cells, and apparently one P_1 cell gave rise to the vitelline membrane. On the other hand, in *Paragonimus kellicotti*, *Parorchis acanthus*, *Fasciolopsis buski* and *Megalodiscus temperatus*, the P cell remained undivided while the E cell divided repeatedly giving rise to two or three cell types, one of which gave rise to the vitelline membrane. In *Fasciolopsis buski*, *Paragonimus kellicotti*, and *Parorchis acanthus*, the P cell did not divide until after the vitelline membrane had formed, whereas in *Megalodiscus temperatus* the propagatory cell divided just before the formation of the vitelline membrane, but did not contribute to this membrane.

In *Neodiplostomum intermedium* the pronuclei passed directly into the first division without the formation of a resting fusion nucleus as observed in *Paragonimus kellicotti*, *Parorchis acanthus*, *Fasciolopsis buski* and *Megalodiscus temperatus*.

(*b*) *Hatching of the egg*

When the miracidium was fully formed, the egg contained, besides the miracidium, the living vitelline membrane against, but not attached to, the shell, a few, usually two, large remnants of the vitelline cells containing granules and a number of small droplets on the surface of these remnants. There was neither thickening nor deposit on the vitelline membrane over the operculum comparable with the 'mucoid plug' of other species.

For some time prior to hatching the elongate miracidium lay bent on itself within the egg with its apical papilla thrust against the vitelline membrane over the operculum (Fig. 5*a*), occasionally elongating and contracting, brushing its apical papilla over the vitelline membrane, turning around within the egg, or lashing its cilia.

As the time of hatching approached, the slowly flickering flame cells became more and more active, suggesting that the osmotic tension of the egg contents had decreased. The miracidium became more active, elongating and contracting, and revolving slowly about its long axis, frequently causing the vitelline remnants to break up into several parts. A few minutes before hatching, the anterior end of the miracidium was retracted and invaginated almost to the border of the second tier of epidermal plates, the cilia quivered but did not lash, and the posterior end was retracted slightly (Fig. 5*b*).

Suddenly, the operculum opened and the miracidium, surrounded by the intact vitelline membrane, was partially ejected from the egg (Fig. 5*c*). Following this initial explosive partial ejection, the rest of the vitelline membrane and miracidium was slowly extruded until only the aboral end of the vitelline membrane was attached to the rim of the opercular opening. As soon as the miracidium was partially ejected, its cilia began to lash vigorously, and once the vitelline membrane was fully extruded, the miracidium swam about rapidly, repeatedly probing the elastic vitelline membrane with its apical papilla in an attempt to escape. When first extruded, the volume of the vitelline membrane approximated that of the egg, but within a few minutes it had decreased noticeably so that the contained miracidium had less freedom of movement than before. After several minutes spent vigorously probing, the miracidium succeeded in piercing the vitelline membrane, usually at the slightly thinner aboral end, and slowly dragged itself free by vigorous lashing of the cilia (Fig. 5*d*). As the miracidium struggled free, the lip of the rupture in the vitelline membrane was contracted about the body of the miracidium; once the miracidium was free, the vitelline membrane contracted, closing the rupture, so that neither vitelline remnants nor droplets escaped. The vitelline membrane then shrank slowly, but had not disintegrated in 2 hr., the longest period of observation. Before hatching, the granules in the vitelline remnants were fixed in position, but after hatching the granules danced

about, indicating that the vitelline remnants are solid (gel ?) before hatching but liquid (sol ?) after hatching.

From these observations, three points emerge. First, the increase in activity of the flame cells prior to hatching points to a dilution in the osmotically active contents of the egg, presumably caused by either the intake of water or the escape

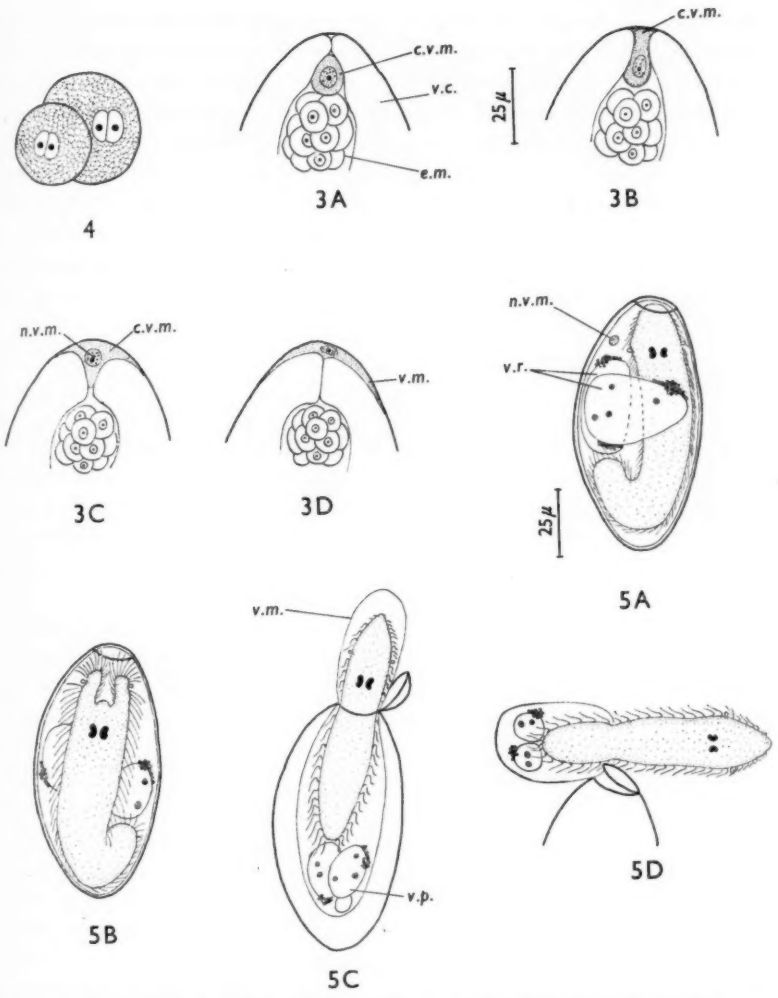

Fig. 3. Formation of vitelline membrane. A, vitelline membrane cell of P_1 type separating from embryo; B, vitelline membrane cell separated from embryo; C, flattening against shell; D, flattened against shell.

Fig. 4. Two-celled stage with double nuclei.

Fig. 5. Hatching of egg. A, attitude of fully developed miracidium; B, invagination of anterior end prior to hatching; D, initial, explosive phase; E, escape from vitelline membrane.

of salts (electrolytes). Secondly, the behaviour (i.e. the invagination of anterior end) of the miracidium immediately before hatching, shows that the miracidium does not force open the operculum, but instead prepares to be ejected. Thirdly, the extrusion of the intact vitelline membrane makes it probable that hypertonicity of the fluid between vitelline membrane and shell is an important part of the mechanism of hatching.

It is generally agreed that hatching of trematode eggs results from a combination of hypertonic egg contents and the release of a hatching enzyme that dissolves the opercular junction (Rowan, 1956, 1957). There are, however, interesting differences in the succession of events at hatching. For example, the vitelline membrane may rupture over the opercular opening, so that the miracidium escapes directly as described by Pearson (1956) for *Alaria arisaemoides*; or the vitelline membrane may rupture and a mucoid plug be extruded as a membrane through which the miracidium must escape, as described by Rowan (1956) for *Fasciola hepatica*; or the miracidium may be expelled within the intact vitelline membrane, as in dicrocoeliids (Maldonado 1945), spirorchiids (Wall, 1941*a*, *b* 1951), and as described above in *Neodiplostomum intermedium*.

(*c*) *Morphology*

Four miracidia fixed in hot 0·5% silver nitrate ranged in size from $73 \times 28 \mu$ to $85 \times 30 \mu$. The body is clavate, being rounded at both ends and widest in the anterior half, and is covered by twenty-two ciliated epidermal plates in four tiers according to the formula 6:9:4:3 (Figs. 6, 10, 11). The first tier consists of six triangular plates, two lateral, two subdorsal and two subventral, with their concave tips forming a ring about the base of the apical papilla, and their bases at about the level of the eyespots (Fig. 9). The second tier consists of nine rectangular plates of which four are dorsal, two roughly lateral, two subventral and one midventral. The third tier consists of four large, almost square, well-separated plates of which two are dorso-lateral and two ventro-lateral. The fourth tier consists of three plates, of which one is dorsal and diamond-shaped and two are subventral and triangular. The epidermal plates are uniformly ciliated, with the cilia in longitudinal rows; the cilia on the last three tiers are about 9·5 μ long, while the cilia on the first tier are short anteriorly and increase to about 9·5 μ posteriorly. Each epidermal plate has a large nucleus which is oval in face view and plano-convex in lateral view. These nuclei, which are arranged as shown in Fig. 10, were seen in fully developed miracidia within eggs, in hatched miracidia under phase contrast, and in a miracidium vitally stained with toluidine blue.

The apical papilla is a low, deformable mound, roughly circular in face view, bounded by the apices of the first tier of epidermal plates. The surface of the apical papilla bears a number of short hairs, with a few longer hairs laterally; these hairs were immobile and are probably sensory. In eight miracidia fixed in silver nitrate and mounted *en face*, twenty pore-like circles were seen arranged in a constant pattern (Fig. 9). The significance of all of these circles is not clear, as only the lateral pair were seen in living miracidia, where they mark the openings of the

cephalic glands. The two groups with eight circles in each may be the multiple openings which the apical gland appeared to possess.

In living miracidia as well as in those fixed in silver nitrate, a variety of structures, presumably sensory, are found between the epidermal plates. These comprise (i) a large, clavate lateral papilla of homogeneous appearance on each side, just above

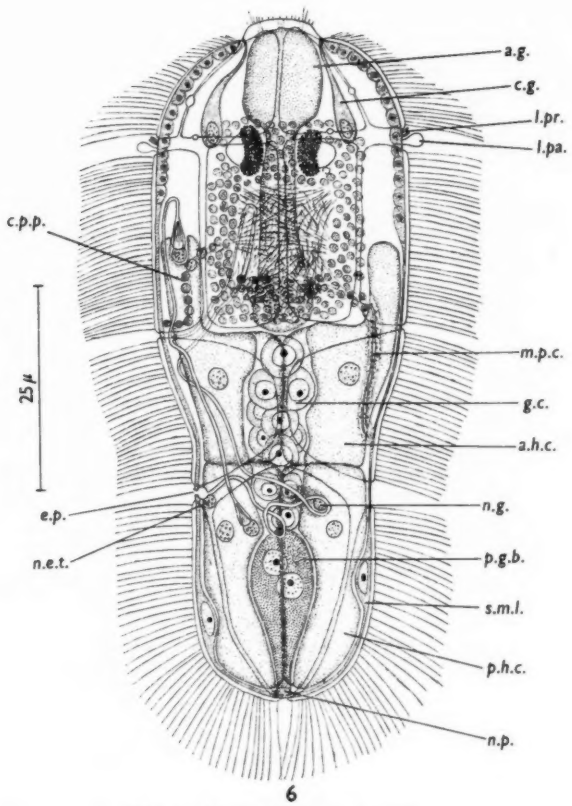

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Fig. 6. Miracidium, dorsal view.

the mid-lateral line between the plates of the first and second tiers; (ii) a short, slender, flexible process immediately dorsal to each lateral papilla; and (iii) six similar processes arranged each in an indentation in the middle of the posterior margin of each plate of the first tier. These processes appear as black circles in miracidia fixed in silver nitrate, whereas the lateral papilla is unaffected by the silver. In living miracidia, a dome-shaped papilla with a corona of about fifteen radiating rays is found on each side between the posterior ends of the lateral and latero-ventral plates of the second tier. What appeared to be a nerve commissure runs from this papilla to the brain (Fig. 12). This papilla appears as a black circle in miracidia fixed in silver nitrate. In both living miracidia and those fixed in

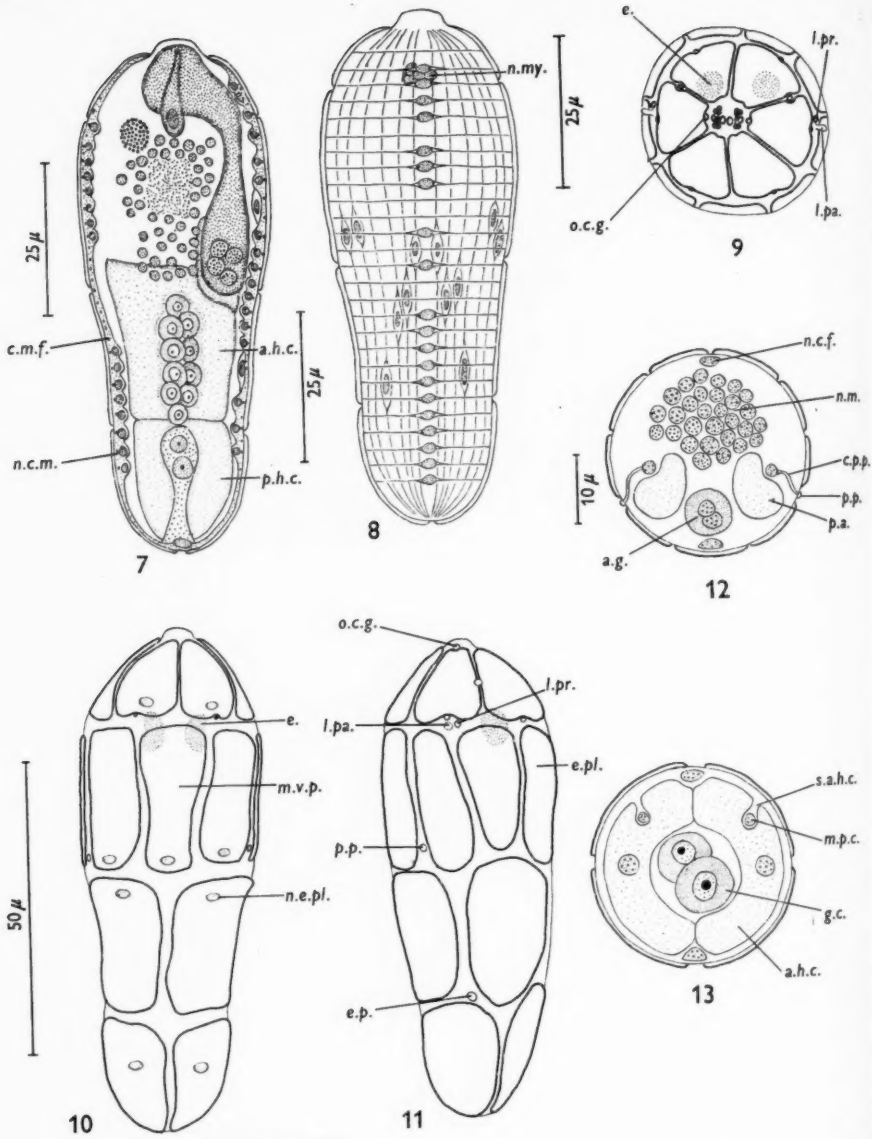


Fig. 7. Miracidium, lateral view.

Fig. 8. Miracidium, dorsal aspect, showing musculature of body wall.

Fig. 9. Miracidium, *en face* view, fixed in silver nitrate.

Fig. 10. Miracidium, ventral aspect, showing epidermal plates.

Fig. 11. Miracidium, lateral aspect, showing epidermal plates.

Fig. 12. Miracidium, optical section of second tier at level of postero-lateral papillae.

Fig. 13. Miracidium, optical section of third tier.

silver nitrate, a black circle is seen on each side between the lateral and subdorsal plates of the first tier.

Beneath the cuticle, on which lie the epidermal plates, are the muscle layers, an outer circular and an inner longitudinal (Fig. 8). The circular fibres are separate; their transversely oval nuclei form two longitudinal, interrupted rows, one mid-dorsal and one mid-ventral, extending from in front of the eyespots to behind the level of the excretory pore (Fig. 7). Internal to the anterior ends of these two rows of nuclei, lie small groups of similar nuclei not associated with circular fibres; these may be the nuclei of myoblasts which will multiply during the transformation of the miracidium into the elongate mother sporocyst. The two rows of nuclei appear at first glance to belong to chains of small cuboidal cells. Hence, the chains of cuboidal cells described in other miracidia by Price (1931), Wall (1941*a*, *b*; 1951) and Pearson (1956) are probably the nuclei and cell bodies of the circular muscle fibres. The longitudinal musculature comprises about twenty-five well-separated bipolar fibres with cell bodies usually in pairs, extending from the base of the apical papilla to the posterior end, with their oval nuclei in a broad equatorial band. The cell bodies of the longitudinal fibres are not fixed to the body wall but are free to move with respect to the circular fibres. The nuclei of both circular and longitudinal muscle cells are dense, and appear to lack nucleoli. A pair of laterally placed retractors of the apical papilla were dimly seen running back into the body on either side of the apical gland.

Beneath the muscle layers lies a single layer of parenchymal cells, with widely separated nuclei posteriorly (Fig. 6). The large number of small parenchymal cells shown in Fig. 6 anterior to the hyaline cells was never seen clearly. Study of many living miracidia suggests that this may be a misinterpretation resulting from the flattening of miracidia, and that the parenchyma is everywhere composed of a small number of large cells. A narrow body cavity separates this layer from the internal organs, except the attached ends of the apical gland and the posterior granular body. The body cavity is much narrower than shown in Fig. 6, which is semi-diagrammatic.

The apical gland is a single cell with four coarsely granular nuclei, without nucleoli, floating freely in fluid or semi-fluid, finely granular cytoplasm which stains purplish with toluidine blue; it arises from and is attached to the apical papilla, has a dilated part anterior to the brain and eyespots, a narrow neck ventral to the brain and a small posterior dilatation ventral to the anterior germinal cells. The four nuclei are usually in the posterior dilatation, but shift back and forth freely during movements of the miracidium. The apical gland apparently opens on the apical papilla through a series of at least nine, probably more, slender ducts. The numerous ducts probably open through some, or all, of the eight pairs of small pores on the apical papilla, although this was not demonstrated. As the apical gland was considerably smaller in day-old mother sporocysts (Fig. 14) it is probably a penetration gland as demonstrated by Mattes (1949) in the miracidium of *Fasciola hepatica*.

Attached to the posterior end of the body is a clavate, coarsely granular body, apparently a single glandular cell, with two large granular nuclei with large

nucleoli. No opening of this gland was seen in five miracidia fixed in silver nitrate and mounted tail up. This structure, called the posterior granular body by Pearson (1956), does not open to the outside, is not used up in penetrating the snail host, and does not contribute to the germinal material (*vide* miracidium-mother sporocyst transformation). In one miracidium, this body was in two parts, each with a nucleus, suggesting that the binucleate structure is formed by the fusion of two cells.

On either side of the apical gland lies a small, slender, flask-shaped, unicellular gland cell, the so-called cephalic gland, with finely granular cytoplasm and dense nucleus: each cephalic gland opens through a pore on the side of the apical papilla at the tip of the lateral plate of the first tier.

A pair of separated eyespots, each comprising a pigment granule cup and a single lens, lies dorsally at about the junction of first and second tiers of epidermal plates. Behind the eyespots lies the brain, or neural mass, a cuboidal aggregate of non-nucleated fibres surrounded by several layers of nuclei. On each side a commissure arises and runs postero-ventrally to the postero-lateral papilla between the plates of the second tier. Postero-laterally, a commissure arises on each side, runs back in a dorso-lateral longitudinal groove (Fig. 13) in the anterior hyaline cell, and appears to terminate on the body wall. No commissures or fibres were seen running from the brain to lateral papillae, lateral processes or apical papilla.

A fusiform group of seven to eleven large germinal cells, with large nuclei containing a prominent nucleolus and a few granules, lies between the brain and the posterior granular body, separated from the body wall by the anterior pair of hyaline cells. Study of the developing mother sporocyst has shown that there is no increase in this small number of germinal cells.

Whereas in other strigeoid miracidia the germinal cells and posterior granular body lie in a cavity, in the miracidium of *Neodiplostomum intermedium* both of these structures are enclosed by two pairs of large hyaline cells. These cells have homogeneous, clear cytoplasm and a small granular nucleus which lacks a nucleolus. The main portion of the anterior pair corresponds roughly with the limits of the third tier of epidermal plates, and the two cells together form a thick-walled tube enclosing the germinal cells (Fig. 13). Each anterior hyaline cell has a ventro-lateral extension which runs forward to the anterior flame cell at about the mid-point of the second tier, and a dorso-lateral longitudinal sulcus containing the main posterior commissure from the brain. The posterior pair of hyaline cells extends from the anterior pair to the posterior end and encloses the posterior granular body.

In older free-swimming miracidia and in miracidia which had penetrated limpets, the hyaline cells had broken up or disappeared. At this time a few slender strands of hyaline cell substance could be seen running to the body wall, and serving presumably to anchor the hyaline cells.

The excretory system is composed of two separate parts and has the formula $2[1+1]$, which is characteristic of strigeatoids as shown by La Rue (1957). As both sides are similar, only one side will be described. The fixed, circular, permanently open excretory pore lies in the space bounded by the dorso- and ventro-

lateral plates of the third tier and the subventral plate of the fourth tier. The pore opens into a small bladder, from which the long primary tubule arises. The primary tubule runs dorsally over the the posterior hyaline cell, forms two or more loops which may overlap those of the other side, runs antero-laterally over the anterior hyaline cell on the same side, bends ventrally passing around the anterior extension of the anterior hyaline cell, runs anteriorly beside the apical gland almost to the eyespots, then turns back on itself to form an anterior loop, and divides at the side of the body into anterior and posterior secondary tubules. The anterior tubule runs forward to the anterior flame cell, which is directed anteriorly and lies dorso-laterally against the anterior end of the anterior hyaline cell. The posterior tubule runs back dorsally to the anteriorly directed posterior flame cell lying dorsal to the posterior hyaline cell just behind the level of the excretory pore. In addition to the flame cell nuclei, two other nuclei were associated with the excretory tubules on each side, one on the wall of the bladder and the second on the posterior loop of the primary tubule. The second nucleus was associated with an ill-defined granular body, possibly a paranephrocyte, similar to that described by Pearson (1956) in the miracidium of *Alaria arisaemoides*.

(*d*) *Comparison*

The morphology of the miracidium of *Neodiplostomum intermedium* agrees generally with the picture of the strigeoid miracidium which has emerged from the studies of Hunter & Hunter (1935) on *Uvulifer ambloplitis*, Odlaug (1940) on *Alaria intermedia*, Pearson (1956) on *A. arisaemoides*, Park (1936) on *Neodiplostomum lucidum*, Chandler (1942) on *N. texensis*, van Haitsma (1931*b*) and Cort, Ameel & Van Der Woude (1951) on *Diplostomum flexicaudum*, Mathias (1925) on *Strigea tarda* (= *Cotylurus cornutus*), Yamaguti (1940) on *Strigea elongata*, *S. falconis*, and *Neodiplostomum cochleare*, Yamaguti (1940) & Hugghins (1954*a*) on *Hysteromorpha triloba*, Sewell (1922) on the miracidium of Cercariae Indicae XV, Tang (1941) on *Prosostephanus industrius* and Anderson & Cable (1950) on *Linstowiella szidati*.

The miracidium of strigeoids is essentially like that of clinostomatoids as shown by Hunter & Hunter's (1935) description of the miracidium *Clinostomum marginatum*. It also resembles that of schistosomatoids, as revealed by the studies of Price (1931) on *Schistosomatium douthitti*; Cort (1919) and Faust & Hoffman (1934) on *Schistosoma mansoni*; Cort (1919), Faust & Meleney (1924), Tang (1938) and Ozaki (1952) on *S. japonicum*; Reisinger (1923) and Porter (1938) on *S. haematobium*; Wall (1941*a*) on *Spirorchis elephantis*; Wall (1941*b*) on *S. parvus*; Wall (1951) on *Vasotrema robustum*; Pieper (1953) on *Spirorchis artericola*; Penner & Wagner (1956) on *Ornithobilharzia canaliculata*; Chu & Cutress (1954) on *Austrobilharzia variglandis* and Bearup (1956) on *A. terrigalensis*.

One of the controversial points in the morphology of the strigeate miracidium is the number of epidermal plates. All authors are agreed that there are four tiers, but various epidermal plate formulae have been proposed, ranging from 6:6:4:2 = 18 in *Spirorchis* spp. and *Vasotrema robustum*, through 6:6:6:3 = 21 in *Uvulifer ambloplitis* and 6:8:4:3 = 21 in the majority of species, to 6:9:4:3 = 22 in

Schistosoma japonicum as described by Ozaki (1952), *Ornithobilharzia canaliculata*, *Alaria arisaemoides*, *Neodiplostomum lucidum*, *N. texensis* and *N. intermedium*. While it cannot be stated categorically, it seems likely that the formula 6:9:4:3 = 22 is the correct one and will be found throughout the strigeate trematodes. Error in ascertaining the epidermal plate formula could arise by assuming that the plates of the second tier are arranged symmetrically in pairs about the mid-sagittal plane, whereas, in fact, there is a mid-ventral, unpaired plate.

With regard to lateral penetration glands, it has generally been assumed that in schistosomatoid miracidia, a pair of glands, the so-called cephalic glands, were present in addition to the apical gland, but that they were absent in strigeoid miracidia, with the exception of that of *Uvulifer ambloplitis*. The finding of such penetration glands, however, in the miracidium of *Neodiplostomum intermedium* suggests that they may be of more widespread occurrence among strigeoid miracidia. Further, the occurrence of such a pair of gland cells in a wide variety of miracidia belonging to several families suggests that they may be a feature common to miracidia generally. It seems likely, from the observations of Mattes (1949) on the miracidium of *Fasciola hepatica*, that the lateral gland cells produce an adhesive rather than histolytic secretion.

It appears from the literature that the body wall musculature has not been fully described previously for any strigeate miracidium. A number of authors have mentioned the presence of circular and longitudinal fibres, but none has described the nuclei of the fibres. In this regard it may be pointed out that the so-called dorsal chain of nuclei in the miracidia of *Schistosoma japonicum* described by Tang (1938), *Schistosomatium douthitti*, *Spirorchis parvus*, *S. elephantis*, *Vasotrema robustum*, and *Alaria arisaemoides* probably represents the nuclei of the circular fibres. Also the lateral pairs of germinal cells, each with an anterior and a posterior process, in the miracidium of *Hysteromorpha triloba* as described by Hugghins (1954*a*) may be paired longitudinal muscle cells.

Nothing comparable with the four hyaline cells of the miracidium of *Neodiplostomum intermedium* has apparently been described before for any strigeate miracidium, in most of which the germinal cells lie in the body cavity. In gross appearance, the hyaline cells of the miracidium are like the caudal bodies of the cercarial tail and may be glycogen stores as shown recently by Erasmus (1958) for the caudal bodies of a diplostomatid, *Cercaria X*.

The posterior granular body, a multinucleate cell of glandular appearance, is present in the miracidia of *Neodiplostomum intermedium* and *Alaria arisaemoides*, and a similar structure has been described in the miracidia of *Diplostomum flexicaudum* by van Haitsma (1931*b*), *Neodiplostomum lucidum*, and *Hysteromorpha triloba* by Hugghins (1954*a*), in which three species it was considered to be a posterior group of germinal cells. Studies on the early development of the mother sporocyst of *Diplostomum flexicaudum* by Cort *et al.* (1951), of *Alaria arisaemoides* by Pearson (1956), and of *Neodiplostomum intermedium* described below have shown that, in these three species at any rate, the posterior granular body does not contribute to the germinal material of the mother sporocyst. At present, the function of this cell of glandular appearance is problematic.

It is interesting to note that the so-called brain, ganglion, or neural mass is considered by Chu & Cutress (1954) to be neither nervous nor glandular on the basis of their observations on the miracidium of *Austrobilharzia variglandis*. Considering the great difference between the complex activities of the miracidium (hatching, swimming, penetration of snail, and localization within the snail) and the simple activities of the mother sporocyst (sluggish crawling, feeding by osmosis), it seems reasonable to assume that the miracidium possesses a more complex nervous system than does the mother sporocyst, and that this complex system would degenerate in part during transformation into a mother sporocyst.

It appears likely, despite the observations of earlier workers, that the apical gland opens through a number of pores on the apical papilla, since multiple openings are apparently present in the miracidium of *Neodiplostomum intermedium*, *Hystomorpha triloba* described by Yamaguti (1940) and Hugghins (1954*a*) and *Schistosoma haematobium* described by Reisinger (1923), as well as in the distantly related miracidium of *Heronimus chelydrae*, a paramphistomatoid according to Cable & Crandall (1956), as described by Lynch (1933).

V. MOTHER SPOROCYST

The early development of the mother sporocyst was studied in living specimens from experimentally infected, laboratory-reared limpets. As very young limpets were used to facilitate recovery of early stages, the rate of development described below is probably slower than in fully grown limpets.

The youngest mother sporocysts examined were 1 day old (Fig. 14); these were found in the peri-hepatic haemocoele, which bathes the organs of the visceral hump. In the living limpet, these young mothers could be seen crawling sluggishly among the acini of the digestive gland. The epidermal plates, apical hairs, lateral papillae, lateral processes, and postero-lateral papillae were absent; the posterior granular body was present and apparently unaltered; the apical gland was greatly reduced in size but still contained four nuclei of normal appearance; the hyaline cells had disappeared, apparently freeing their nuclei, and leaving a large fluid-filled cavity about the germinal cells; the eyespots had separated and begun to disintegrate; the neural mass had shifted and begun to disintegrate, assuming as it did so the form of a long, loosely folded tape bearing many pycnotic nuclei; the number of flame cells and the arrangement of their capillaries had not altered. The germinal cells, still forming a single group of cells attached to one another, had begun to divide and in one day-old mother sporocyst eighteen cells were seen, while in another the number of cells increased from thirteen to sixteen during the period of observation. Observations given below on older mother sporocysts have shown that there is no increase in the number of germinal cells from miracidium to fully developed mother sporocyst; hence, the new cells formed in the day-old mother sporocyst must have been the anlagen of the multicellular elements of germinal masses, i.e. daughter sporocyst embryos.

Two-day-old mother sporocysts had grown very little, had an unaltered posterior granular body, a remnant of the apical gland, no trace of the neural mass, and the

germinal cells and their division products organized into four germinal masses. In developing daughter sporocyst embryos within germinal masses, there were three types of nuclei comparable with the nuclei of the E, P, and P_1 cells of the developing miracidium. The cells lining the body cavity had increased in number.

Five-day-old mother sporocysts had increased in length to about 350 μ, had small remnants of apical gland and posterior granular body, and contained four germinal masses and one or more spherical free daughter sporocyst embryos (Fig. 15).

By 7 days, no trace of apical gland or posterior granular body was seen, the number of flame cells had increased, and the body cavity contained four germinal masses and many free daughter sporocyst embryos, some of which contained germinal masses and free cercarial embryos.

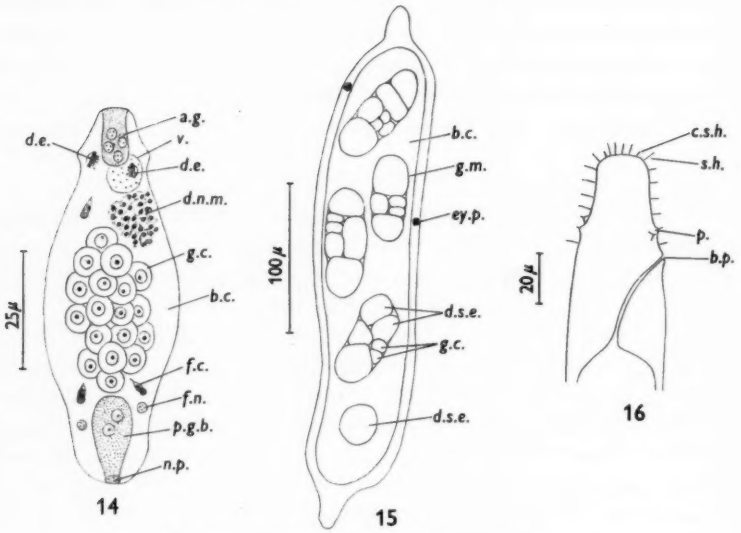


Fig. 14. One-day-old mother sporocyst.
Fig. 15. Five-day-old mother sporocyst.
Fig. 16. Anterior end of daughter sporocyst.

Mother sporocysts continued to grow after daughter sporocysts had begun to escape, and by 5 weeks after infection had attained lengths ranging from 720 to 900 μ. The fully developed mother sporocyst was always found in the haemocoele of the visceral hump, crawling actively among acini of the digestive gland and daughter sporocysts. The mother sporocyst is an elongate hollow sac; its body wall consists of a cuticle without sensory hairs, separated bipolar circular and longitudinal muscle cells, and a single layer of large stellate cells with vesicular nuclei each with a large nucleolus, next to the body cavity. Scattered among the stellate submuscular cells and bulging into the lumen of the cavity, are larger cells which contain numerous, conspicuous, active mitochondria. These larger cells may be associated with the absorption of food from the haemocoele.

Fully developed mother sporocysts contained four germinal masses and these, in turn, contained a total of seven to twelve germinal cells, i.e. the number present in the miracidium. There was not, then, any multiplication of germinal cells during the formation of the mother sporocysts; on the contrary, the seven to eleven germinal cells of the miracidia were apparently already grouped into four incipient germinal masses. A similar pattern of germinal development is present in *Alaria arisaemoides*, where the miracidium with seventeen germinal cells develops into a mother sporocyst with about eight germinal masses (Pearson, 1956). In *Diplostomum flexicaudum*, on the other hand, Cort *et al.* (1951) found that the miracidium, with eight germinal cells, developed into a mother sporocyst with twenty to twenty-four germinal masses.

VI. DAUGHTER SPOROCYST

Daughter sporocysts first escaped from the mother sporocyst some time after the seventh day and were releasing cercariae by the nineteenth day at summer temperatures. Ten daughter sporocysts from a limpet infected 5 weeks earlier ranged in length from 590 to 850 μ. The daughter sporocyst is an elongate, hollow muscular sac, rounded posteriorly and slightly attenuated and solid anteriorly, with subterminal birth pore and body cavity packed with about twelve germinal masses and many cercarial embryos. The body wall is like that of the mother sporocyst; the cuticle bears a subterminal ring of four papillae, each with a short hair, and a number of fine hairs scattered over the anterior end (Fig. 16). Most of these hairs were motionless, but those in a circle about the tip lashed vigorously in the manner of cilia. Close observation of living daughter sporocysts mounted in methyl cellulose showed that this was not due to Brownian movement as only the hairs in the apical circle lashed, while the other hairs remained motionless.

The presence of structures resembling cilia is surprising in view of the generally held opinion that the daughter sporocyst has lost its epidermis. Immobile hairs are present on the daughter sporocysts of several species of strigeatoids, but lashing, cilia-like hairs have apparently not been described. It may be noted in this connexion that the caudal sensory hairs of the cercaria were occasionally observed lashing slowly as cercariae flattened and died in drying wet mounts.

VII. CERCARIA

(*a*) *Diagnosis*

The diagnosis and description are based on the study of both living cercariae and those fixed in formalin and cleared in glycerine; measurements (average and range) are given in microns for ten fixed specimens.

Furcocercous, longifurcous, distomate, pharyngeate (Fig. 17). Body elongate, constricted anterior to ventral sucker in fixed material, with five constrictions between gut bifurcation and ventral sucker in living material; length 160 (123–190) μ and width 34 (30–40) μ; with two pairs of sensory hairs, an anteriorly directed pair dorsally at anterior end and a posterolateral pair. Oral sucker large, with subterminal opening and large cavity; tip invaginable, not retractile; without internal gland cells; length 36 (31–44) μ and width 25 (22–31) μ. Prepharynx short, length 3·5 (2·5–5·5) μ. Pharynx small, 12 (11–16) μ long and 15 (12–18) μ

wide. Oesophagus long and slender, length 24 (23–25) μ; bifurcation of gut about midway between pharynx and ventral sucker. Caeca thin-walled, inflated, permanently septate with five pouches in each caecum, extend to just behind ventral sucker. Ventral sucker smaller than oral sucker, length 21 (20–24) μ and width 22 (18–29) μ, with posterior margin 37 (28–42) μ from posterior end of body; mouth of ventral sucker opens into shallow invagination of ventral surface (Fig. 18). Two pairs of coarsely granular penetration glands, with irregular margins in living cercariae; one pair in front of, or overlapping, ventral sucker and dorsal to caeca with median lobes between caeca; second pair posterior to ventral sucker and ventral to ends of caeca; ducts on each side pass forward, enter posterior face of oral sucker dorso-laterally, are dilated proximally, and open one above other at sides of pre-oral spines. Oval, undifferentiated genital rudiment between ends of caeca and excretory bladder. Pair of small, dense, rounded bodies, one on either side halfway from gut bifurcation to ventral sucker, may be comparable with so-called unpigmented eyespots of other species.

Tailstem 224 (189–262) μ long and 32 (24–41) μ wide; sides parallel, with about sixty annular constrictions; bearing, except in mid-dorsal and mid-ventral spine bands, numerous long, slender, flexible sensory hairs as long as width of tailstem. Furcae simple, without finfolds, length 193 (177–231) μ; with one short sensory hair on lateral face near tip and many short sensory hairs on medial face.

Flame-cell formula 2 [(1 + 1 + 1) + (1 + 1 + (1)] (Fig. 17); bladder bicornuate; each bladder-arm dilated at bladder and convoluted behind ventral sucker, with three ciliary tufts in convoluted part, giving rise before convolutions to anterior blind tubule (rudiment of reserve excretory system) which runs forward beside anterior collecting tubule almost to level of third flame cell; excretory atrium present at tail base; island of Cort absent; pair of caudal flame cells at base of tail stem; caudal excretory tubule runs along ventral face of tailstem between about six pairs of stellate caudal bodies; furcal excretory tubules open mid-furcally on dorsal edge.

Pre-oral area with nine forward-pointing spines in two staggered rows; oral hood of about ten rows of large spines, over first quarter of oral sucker. Dorsally, scattered body spines from oral hood to about level of gut bifurcation; ventrally, the same anterior to ventral sucker, but with two lateral patches of scattered spines behind ventral sucker; body spines decrease in size posteriorly. Ventral sucker bears about fifty inwardly directed spines in two staggered rows. Tailstem with band of spines mid-dorsally and mid-ventrally which continue along full length of furcal margins.

Host: Pettancylus assimilis (Petterd) experimental.

The anterior pair of penetration glands were, in all cases, in front of the ventral sucker; the posterior pair were frequently not opposite, but lay one behind the ventral sucker and ventral to the caecum and the other as far forward as the middle of the ventral sucker lateral to the caecum. In living cercariae flattened under a coverslip, the body usually contracted so that the posterior penetration glands were para-acetabular rather than post-acetabular as in fixed cercariae and the median intercaecal lobes of the anterior penetration glands appeared as two median lobes meeting or overlapping in the mid-line (Fig. 18) in the same manner as Chandler (1942) described for the cercaria of *Neodiplostomum texensis*.

(*b*) *Comparison*

The cercariae of two closely related species in the subgenus *Fibricola* have been described; they are the cercaria of *Neodiplostomum texensis* described by Chandler (1942) and that of *N. lucidum* described by West (1935). Both species differ from the cercaria of *N. intermedium* in having both pairs of penetration glands in front of the equator of the ventral sucker. The cercaria of *N. texensis* differs further in lacking pre-oral spines and septate caeca. The cercaria of *N. lucidum* is said to have eight pairs of flame cells in the body, whereas the cercariae of *N. texensis* and *N. intermedium* have only five pairs. It seems likely that three of the flame cells

beside the ventral sucker in West's figure (Pl. III, Fig. 1) were three tufts of cilia in the convolutions of the bladder arm. West says that the bladder arm is not convoluted, a most unusual condition, but admits that he was not able to trace the connexions of the flame cells.

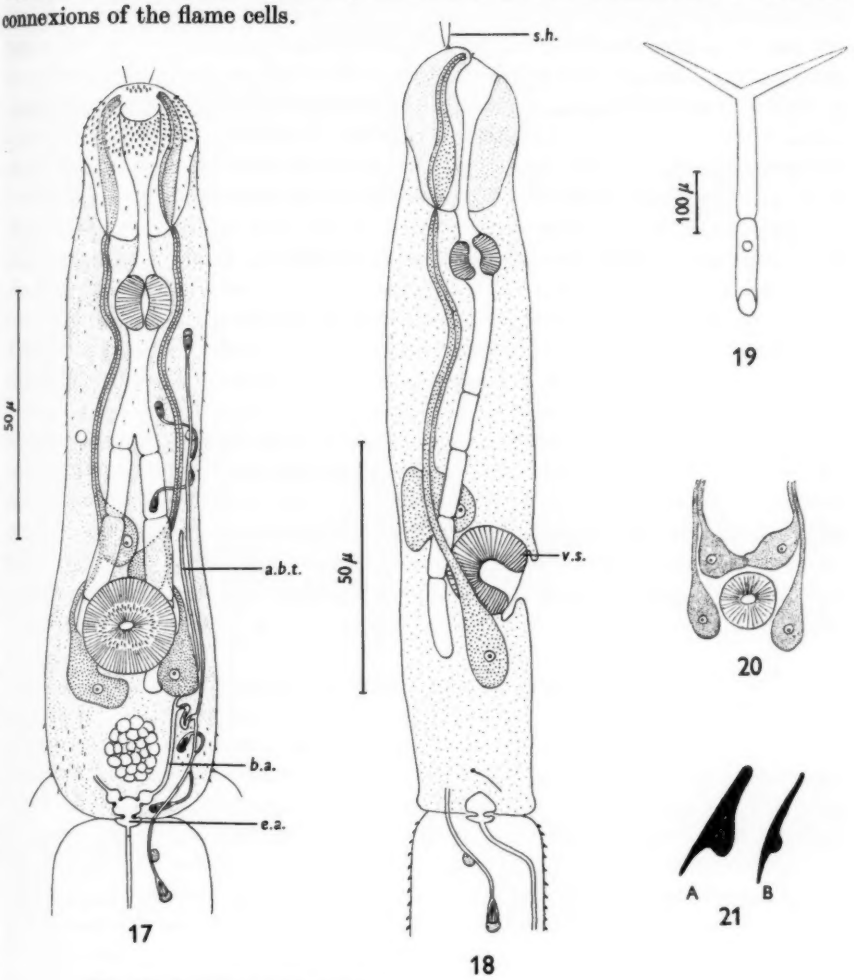


Fig. 17. Cercaria, ventral view.
Fig. 18. Cercaria, lateral view.
Fig. 19. Outline of cercaria, in resting position.
Fig. 20. Arrangement of penetration glands in contracted body.
Fig. 21. Cercarial spines. A, from oral hood; B, from ventral sucker.

Hoffman (1958) reported that *Cercaria kappa* Brooks, 1948 developed in the body cavity of tadpoles into a diplostomulum similar to that of *N. texensis*. Hoffman did not describe either cercaria or diplostomulum, and although Brooks's (1948) brief description of the cercaria is insufficient for positive identification, his

measurements are close to those of the cercaria of *N. craterum* given by Chandler (1942).

A search of the literature has revealed only two species of distomate, longifurcous, pharyngeate furcocercariae, with two pairs of penetration glands arranged one before and one behind the ventral sucker, namely, *Cercaria macradena* and *C. micradena* described by Cort & Brackett (1938*b*). The latter species was shown by Olivier (1940) to be the cercaria of a diplostomatid which he named *Diplostomum micradenum*, but which Dubois (1953) considered to be a synonym of *Hysteromorpha triloba*. In view of the differences in cercarial morphology, snail host, and second intermediate host between *Diplostomum micradenum* as described by Olivier (1940) and *Hysteromorpha triloba* as described by Hugghins (1954*a*, *b*), these two species cannot be considered to be the same. *Cercaria macradena* and *C. micradena* differ from the cercaria of *Neodiplostomum intermedium* in snail host, relation of penetration glands with caeca and flame cell formula. Further, *Cercaria micradena* is the cercaria of a species of *Diplostomum* and *Cercaria macradena* is probably the cercaria of a closely related species, as suggested by Cort & Brackett (1938*b*).

Brooks (1948) briefly described *C. cryptadena* in which there are four penetration glands, the anterior pair in front of the ventral sucker and, in 70% of cases, one member of the posterior pair in front of and the other behind the ventral sucker. This curious arrangement of the penetration glands was observed in some cercariae of *Neodiplostomum intermedium*. However, *Cercaria cryptadena* differs in having two pairs of caudal flame cells and in developing into a metacercaria in fish.

(*c*) *Morphology of tail* (Figs. 22, 23)

(1) *Description.* The tail (tailstem and furcae) is a hollow, fluid-filled, closed tube, bounded by a thick cuticle below which lie circular and longitudinal muscle fibres which are apparently not separated, by parenchyma, from the cavity. The cuticle of the tailstem is thrown into about sixty annular constrictions by the uniformly spaced, anucleate circular muscle fibres, which appear to form closed rings. Circular fibres in the furcae are widely spaced, and many adjacent pairs cross over one another (Fig. 23). The longitudinal muscle fibres are arranged in four discrete groups, two dorsal and two ventral, which extend from the base of the tailstem to the tips of the furcae. Within the furcae the groups run along the lateral face. Individual longitudinal fibres are bipolar, with the cell body, containing the nucleus, bulging into the cavity of the tail and the contractile parts lying beneath the circular fibres. The fibres run back diagonally from lateral to medial edge of each bundle; the fibres are cross-striated, with areas similar to the Z-line, J-disk, and Q-disk of insect muscle fibres and of mammalian voluntary muscle fibres. The striations are for the most part opposite one another over the width of each bundle, again as in insect and mammalian striated muscle. Striated muscle cells in the cercarial tail are uninucleate, whereas those of insects and mammals are multinucleate. Each bundle is composed of about twenty-eight bipolar fibres in the tailstem and a smaller number in the furcae.

Each furca has the two longitudinal bundles from the same side of the tailstem

continuing as separated, laterally flattened bands along the lateral face. On the lateral face in the mid-line between the dorsal and ventral longitudinal bundles lies a single row of uniformly spaced nuclei which belong to circular muscle fibres. Between adjacent pairs of nucleated circular fibres there are four or more circular fibres which appear to lack nuclei. The slender circular fibres run external to the longitudinal fibres and beneath the cuticle. Many of the adjacent anuclear fibres cross one another. On the medial face of each furca there are five separated bipolar, cross-striated muscle fibres which run from the furcal tip to the wall of the furca proximally. There are two rows of well-separated interfacial fibres without nuclei in each furca (Fig. 23). Within the bases of the furcae there is a proximal group of about five interfurcal muscle fibres, the flexors of furcae, which run through the cavity of the tail from the medial face of one furca to the medial face of the other; no nuclei were seen associated with these fibres. In the junction of the medial faces of the furcae lies a group of five bipolar fibres, the extensors of the furcae, the ends of which are inserted mid-dorsally and mid-ventrally on the wall of the tailstem distally.

The cuticle on the medial faces of the furcae proximally is thrown into a series of fine dorso-ventral folds, whereas the cuticle on the rest of the furcae is smooth. This proximal folding apparently provides part of the mechanism whereby the furcae can be flexed to within less than 90° of the tailstem, as they are when a cercaria is swimming tail first. The other part of this mechanism is probably the increase in turgor consequent on the contraction of circular and longitudinal fibres of the tailstem. That there is an increase in turgor is suggested by the observation that, during swimming, the furcae elongate in spite of strong contractions of the longitudinal fibres.

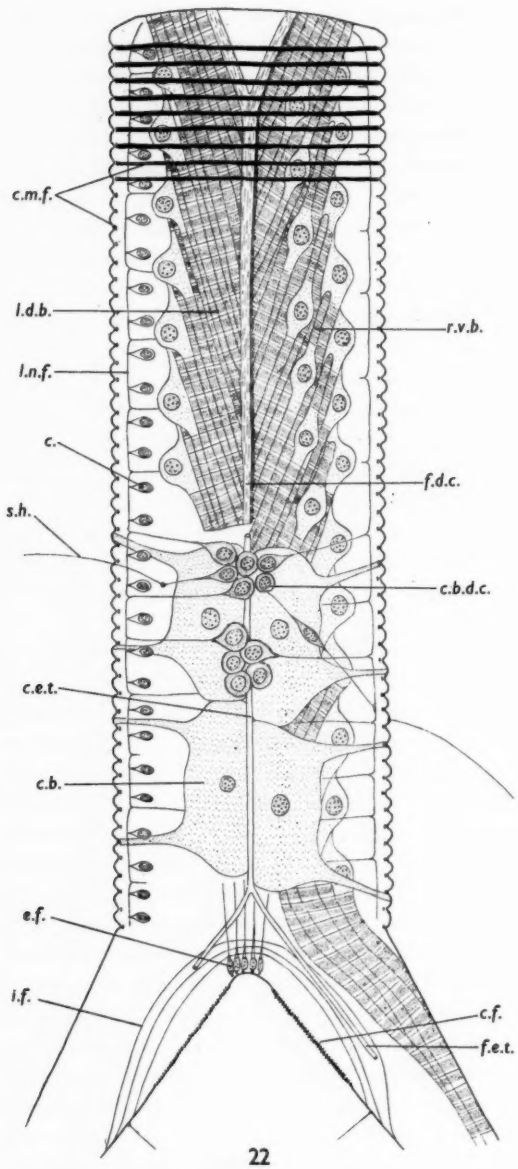
There are two main nerve commissures in the tailstem, one mid-dorsal and one mid-ventral, lying between the longitudinal muscle bundles, with the fibrous part just below the cuticle and circular muscle fibres and the cell bodies internal to this and projecting into the cavity of the tailstem. Many of the irregularly grouped nuclei internal to the fibres belong to bipolar cells which connect the main commissures with one another, with the sensory hairs, presumably with the longitudinal muscle fibres, and with the circular muscle fibres. The bipolar fibres connect with the circular fibres on each side by means of branches to each muscle fibre from a mid-lateral longitudinal nerve fibre running the length of the tailstem and having on its course a series of about thirty small cells. Each main nerve commissure arises proximally by the fusion of branches of the paired main posterior ventral commissures of the body, and each divides distally, sending a branch to each furca. The course and relations of the commissures in the furcae could not be made out.

The union in the tail of the main lateral commissures of the body has presumably been effected by the same moulding of the posterior end of the cercarial embryo that results in the fusion of the originally separate primary excretory tubules.

Internal to the ventral commissure in the tailstem lies the caudal excretory tubule, which is supported laterally by a series of about six pairs of stellate caudal bodies. The processes of the caudal bodies appear to be inserted on the cuticle, not

on subcuticular cells as described by Olivier (1940) for the cercaria of *Apharyngostrigea pipientis*.

(2) *Comparison*. Relatively few descriptions have been given of the musculature



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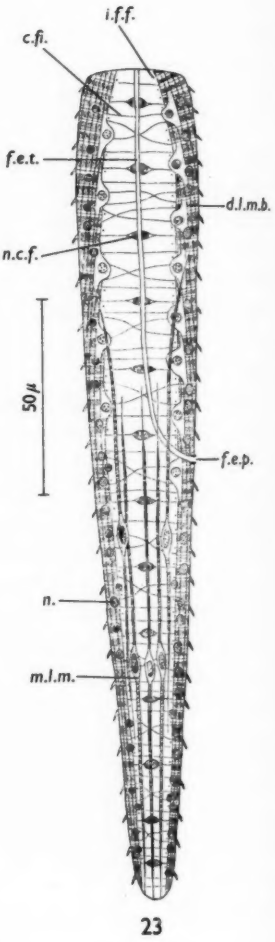

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Fig. 22. Tailstem of cercaria, dorsal view, schematized.

Fig. 23. Furca, medial view (interfurcal fibres and circular fibres on medial face omitted).

of the tail of strigeate cercariae; these include observations by Sewell (1922) on Cercariae Indicae XXV, Olivier (1940) on *Apharyngostrigea pipientis*, Martin (1945) on *Cercaria nassa*, Miller (1926) on several furcocercariae, Price (1931) on *Schistosomatium douthitti*, Tang (1941) on *Prosostephanus industrius*, Wall (1941*a*, *b*) on *Spirorchis elephantis* and *S. parvus*, Pearson (1956) on *Alaria arisaemoides*, and Pearson (1959*a*) on *Strigea elegans*. All of these authors, except Martin, agree that the longitudinal fibres are bipolar, but only Martin (1945) and Pearson (1956, 1959*a*) have described cross-striations.

The cross-striated nature of the longitudinal muscle fibres in strigeate cercariae has been noted by Linton (1915), Martin (1945) and described in more detail by Pearson (1956, 1959*a*). Among non-strigeate cercariae, only one reference to cross-striations has been found, and that in Sinitsin's (1911) description of *Cercaria equitator*, a macrocercous form. It may be remarked here that, according to Hyman (1951, p. 77), muscle fibres in some highly muscular organs of turbellaria show a primitive cross-striation.

Sinitsin (1911) has described in detail remarkable longitudinal muscle cells in the tail of *Cercaria pennata*, a trichocercous form, probably a fellodistomatid. In this cercaria the longitudinal muscle cells are said to be elongate and fusiform, with a large vacuolated cell body and a group of longitudinal fibrils on a part of the external face. The groups of fibrils on the external faces are so arranged that they form four longitudinal bands, suggesting that Sinitsin may have combined longitudinal muscle cells and the internal caudal bodies in his interpretation of cross-sections of the tail.

Haswell (1903) has described in considerable detail the morphology of the tail of a remarkable furcocercaria, possibly an allocreadioid, from *Mytilus latus* in New Zealand. In this unnamed cercaria, the longitudinal muscle fibres in the tail are arranged in four discrete bands, of which two are dorsal and two ventral. Haswell, like Sinitsin, considers that the longitudinal fibres are produced by large myoblasts and does not appear to consider each fibre to be a single cell.

In strigeoids (Miller, 1926; Olivier, 1940; and Pearson, 1956), the longitudinal fibres are arranged in four bands; whereas in schistosomatids (Miller, 1926; Price 1931) there are said to be six or more bands. In spirorchiids, according to Wall and to Sewell, there is a continuous layer of longitudinal fibres spirally wound proximally and straight distally, but according to Miller there are four groups. The writer (unpublished) has seen a somewhat different arrangement in an undescribed spirorchiid cercaria from the snail, *Lenameria* sp., collected in Brisbane. In the tailstem of this cercaria there were separate dorsal and ventral groups of longitudinal fibres which interlaced laterally at the proximal end.

The attachment of the longitudinal fibres in the furcae appears to vary, as in *Apharyngostrigea pipientis* they are inserted on both faces, in *Neodiplostomum intermedium* on the lateral face, and in *Alaria arisaemoides* on the medial face with a separate bundle on the lateral face arising in the tailstem. The dorso-ventral fibres on each face of the furcae in *A. arisaemoides* are probably comparable with the circular fibres in *Neodiplostomum intermedium*. Interfacial fibres, flexor fibres, and extensor fibres have apparently not been described before. The circular fibres of

the tailstem are similarly arranged in *Alaria arisaemoides*, *Strigea elegans*, and *Neodiplostomum intermedium*, but differently arranged in *Apharyngostrigea pipientis* in which they interlace dorsally and ventrally.

The nervous system in the tail of cercariae has apparently received little attention, as only a single reference to this system has been found, namely, Haswell's (1903) description of lateral commissures in the tail of a curious furcocercaria from *Mytilus latus*. This commissure, with its regularly spaced nuclei, is similar to that described above for *Neodiplostomum intermedium*. Haswell apparently did not see mid-dorsal and mid-ventral commissures, nor did he trace the connexions between body and tail.

The groups of nuclei below and between the muscle bands in the tailstem of *Alaria arisaemoides* and the mid-dorsal and mid-ventral rows of cells in the tailstem of *Apharyngostrigea pipientis* are probably a part of the main nerve commissures.

Essentially the same arrangement of muscle fibres and nervous elements has been observed by the writer (unpublished) in the cercaria of a species of *Apatemon* (Fam. Strigeidae) from the limpet, *Pettancylus assimilis*, collected in Brisbane. The only differences noted were (i) the smaller number—four on either side—of cells along the course of the mid-lateral nerve fibre, and (ii) extensions, from some of the cell bodies, of longitudinal fibres to the cuticle laterally.

(*d*) *Escape of cercariae*

Observations on the route and manner of emergence were made on intact, living limpets crawling on the meniscus or lying on their backs in a dish of water. Mother sporocyst, daughter sporocysts and newly emerged cercariae crawled about freely in the large visceral haemocoele, which drains through vessels in the mantle, and presumably the peri-rectal sinus, to the heart. Cercariae crawled about the visceral haemocoele, probing vigorously with the anterior end, and entered the first part of the peri-rectal sinus and the mantle vessels. Of the many cercariae observed trying to escape, all but one of those which were successful escaped by the same route. Successful cercariae entered a mantle vessel which arises ventral to the attachment of the retractors of the foot on the right side, and runs antero-laterally to the edge of the mantle where it courses across to the left side. Once a cercaria had entered this vessel, it crawled quickly along, aided by the flow of blood in the wider portions of the vessel, to a point on the left side antero-laterally where the narrowing of the vessel prevented further advance. At this point, the cercaria vigorously probed the wall of the vessel and in a few seconds had wormed its body through vessel wall and overlying integument. Once the body was free in the water, the cercaria became quiescent and the tailstem and furcae were slowly extruded, like toothpaste from a tube, by the pressure of the blood. In most cases the furcae were completely extruded, but in a few cases the tips of the furcae remained attached until freed by the cercaria attempting to swim. In no case was an emerging cercaria trapped in mucus.

With one exception, all of the cercariae observed emerging from the three limpets examined emerged from the same point. While no permanent wound or

papilla was seen, it appears probable that cercariae create, and maintain by frequent passage, a fixed 'escape pore' on the edge of the mantle. The 'escape pore' is a rupture in the wall of the blood vessel and the overlying integument, which is closed by contraction of the integument after the escape of each cercaria.

The manner in which cercariae of *Neodiplostomum intermedium* escape, is the same as that described for the cercariae of *Alaria arisaemoides* and *A. canis* by Pearson (1956), for the cercariae of *Strigea elegans* and a schistosome by Pearson (1959*a*), and for the cercariae of *Apatemon* sp. and an echinostome, probably *Echinoparyphium* sp., by the writer (unpublished). All seven species escaped in the same manner through fixed points on the mantle, collar, and pseudobranch. This manner of escaping differs from that described by Duke (1952) for the cercaria of *Schistosoma mansoni*. Duke found that cercariae escaped through the rupture of vesicles that had formed about cercariae which penetrated from blood spaces into the integument. Although at variance as to the mechanism of escape, I agree with Duke that daughter sporocysts inhabit haemocoelic spaces, and that cercariae can travel freely via sinuses or veins to the site of emergence. This conclusion is at variance with the view expressed, for example, by Kendall & McCullough (1951) that cercariae travel via lymphatic channels to the site of emergence. The fact that lymnaeids, such as *Lymnaea truncatula*, the host studied by these authors, have colourless blood may have led to calling blood vessels 'lymphatic channels'.

After emerging from the limpet, cercariae of *Neodiplostomum intermedium* spent most of their time lying on the bottom in the resting position, occasionally swimming upwards a few millimetres. In this, the cercaria differs from other strigeoid cercariae, all of which remain suspended at all times, and resembles some spirorchiid cercariae as observed by Wall (1941*b*) and by me (unpublished).

VII. DIPLOSTOMULUM

(*a*) *Diagnosis*

The diagnosis and description are based on the study of living worms, stained whole mounts, and serial sections: measurements (average and range) in microns are given for fifteen stained and mounted diplostomula.

Typical diplostomulum, without lateral sucking cups; with large, foliiform, ventrally concave forebody, length 425 (392–460) μ and width 193 (181–220) μ; small, conical hindbody, length 33 (20–46) μ and width 60 (50–74) μ. Oral sucker terminal, pyriform; opens ventrally without internal gland cells; length 40 (37–43) μ and width 32 (30–34) μ. Prepharynx thin-walled, short, length 10 (4–15) μ. Pharynx oval, length 20 (19–22) μ and width 16 (14–19) μ. Oesophagus thin-walled; length 77 (58–98) μ; bifurcating about halfway from pharynx to ventral sucker. Supra-oesophageal commissure 25 (10–35) μ behind pharynx. Caeca thick-walled, run close to lateral margins of holdfast and end beside genital rudiment in hindbody. Ventral sucker circular, length 36 (34–38) μ and width 37 (34–41) μ, diameter less than length of oral sucker; protrusible, lying in shallow invagination when at rest. Holdfast prominent, elongate, length 93 (82–102) μ and width 43 (35–52) μ when retracted; situated 8·5 (0·0–20·0) μ behind posterior margin ventral sucker, with thin flap of ventral body wall over first 30 (24–43) μ of sulcus; with lobed holdfast gland postero-dorsally. Genital rudiment elongate, oval, length 32 (25–43) μ and width 18 (15–22) μ comprising anlagen of ovary, testes, oötype and Mehlis' gland, and bursal region. Reserve excretory system of diplostomulum type with irregularly rounded to bacilliform excretory granules in terminal and lateral pockets; excretory pore dorsal, subterminal.

Forebody spiny dorsally, with spines larger and more numerous anteriorly, with a spineless area on anterior tip over oral sucker on which open a series of dorsal subcuticular gland cells; ventrally with slender spines over oral sucker (Fig. 28), becoming scales over body from pharynx to ventral sucker, reverting to spines, which are larger laterally behind ventral sucker. Margin of holdfast (ventral face when protracted, sulcus when retracted) thickly set with large spines, larger than those on adjacent body wall; centre of holdfast spineless; hindbody spineless except for group of tiny spines about excretory pore.

Host. Tadpole (natural and experimental) and frog (natural) of *Hyla* sp., tadpole of *Mixophyes fasciolatus* (natural infection), and frog of unidentified leptodactylid (natural infection).

Locality. Mt. Glorious, Queensland, Australia (subtropical rain forest).

Location. Encapsulated in muscles of back, base of tail, and jaws in tadpoles and muscles of back and thighs in frogs.

The living diplostomulum, freed from its host cyst, was active, with a more pronounced hindbody than in fixed material and could protract both ventral sucker and holdfast (Fig. 29). In fixed specimens the holdfast was invariably invaginated, while in living specimens not under pressure the holdfast was usually evaginated. When fully evaginated, the holdfast had the form of a flat—or concave—topped mushroom with a short stalk arising from a circular depression in the ventral surface. The invaginated holdfast was elongated, the evaginated was circular, in face view.

In sections, it could be seen that in the invaginated holdfast, spines were absent from the depths of the sulcus, and that in the evaginated holdfast, the marginal band of spines was on the sides of the holdfast and that the whole of the ventral face was spineless. The cuticle over the ventral face of the holdfast stained less intensely with haematoxylin and erythrosin than the spine-bearing cuticle over the lateral faces. Beneath the cuticle over the ventral face, there is a layer of unicellular gland cells, whose secretion is apparently holocrine. It may be noted here that the so-called holdfast gland appears to be not a gland but a food storage organ. The finer structure of the holdfast gland in this and other diplostomatids is at present being investigated.

(*b*) *Related species*

Relatively few diplostomula without lateral sucking cups have been described; they are the diplostomula of *Neodiplostomum texensis* described by Chandler (1942), and *Pharyngostomum cordatum* described by Wallace (1939), *Diplostomulum joyeuxi* described by Joyeux (see Hughes, 1929*a*), *Diplostomulum putorii* (von Linstow) Hughes, 1929 briefly described by von Linstow (1877), *D. vegrandis* (La Rue) Hughes, 1929 described by La Rue (1917) and Hughes (1929*b*), and *D. sirtali* (Nicoll) Hughes, 1929 described by Nicoll (1912).

The diplostomulum of *Neodiplostomum texensis* differs from that of *N. intermedium* in being smaller, having relatively larger oral sucker, pharynx, and ventral sucker, having more commissures between the main vessels of the reserve excretory system, and occurring free in the coelom of the tadpole host. The diplostomulum of *Pharyngostomum cordatum* differs in lacking spines ventrally behind the holdfast and having a relatively larger pharynx.

Diplostomulum vegrandis and *D. sirtali* were both found in North American snakes, *Thamnophis* spp. While they cannot be identified positively as the diplostomula of any known adult, they probably belong to *Neodiplostomum* emend.

Pearson, as the diplostomula of the North American species *N. craterum*, *N. texensis*, and *N. buteonis* can occur in snakes, as shown by Cuckler (1941), Leigh (1954), and the writer (1960), respectively. *Diplostomulum joyeuxi* and *D. putorii* may also belong in *Neodiplostomum*. Wallace (1939) thought it possible that *Diplostomulum putorii* is the diplostomulum of *Pharyngostomum cordatum*. This supposition was supported by Pearson (1956), but a re-examination of the literature shows that *Diplostomulum putorii* could equally well be the metacercaria of one of the many species of *Neodiplostomum* described from European birds. On morphological grounds, it is not possible from von Linstow's brief description and figure (Fig. 21, Taf. XIV) to identify *Diplostomulum putorii* as the diplostomulum of *Pharyngostomum cordatum*. On biological grounds, *Diplostomulum putorii* could belong to either *Pharyngostomum* or *Neodiplostomum* since diplostomula of both genera can use mammalian transport hosts, as shown by Wallace (1939) for *Pharyngostomum cordatum* and by Cuckler (1940) for *N. craterum*. Diplostomula, presumably belonging to *Neodiplostomum*, were found by Bosma (1934) in the lungs of mink in Michigan and by me (unpublished) in the lungs of foxes in Ontario.

(*c*) *Metacercarial types in* Neodiplostomum

The metacercaria of *N. craterum*, *N. texensis*, and *N. intermedium*, members of the subgenus *Fibricola*, is a diplostomulum with excretory granules in blind pockets, as is that of *N. buteonis*, of the subgenus *Neodiplostomum*. On the other hand, the metacercaria of *N.* (*Conodiplostomum*) *perlatum*, described by Ciurea (1930), is a typical neascus with the excretory granules floating freely in the channels of the reserve excretory system, a character which places this form with certainty in the larval group *Neascus*, as defined by Hughes (1927). It follows from this that the larval group *Neascus* does not correspond with a natural group within the family Diplostomatidae, since it includes metacercariae of *Uvulifer*, *Crassiphiala*, *Posthodiplostomum*, and *Neodiplostomum* (in part), genera belonging to two distinct phylogenetic lines. That *Neascus* is not a natural group is perhaps not surprising if, as Pearson (1956) suggested, the patterns of the reserve excretory systems of diplostomatid metacercariae represent various arrested stages in the development of the adult condition.

Dubois (1938, footnote p. 253) has proposed the larval group name *Neodiplostomulum* for the metacercariae of *Neodiplostomum* spp. A name for those diplostomula which lack lappets is perhaps wanted, but the fact that the metacercariae of *Neodiplostomum* spp. belong to two larval groups, *Neascus* and *Diplostomulum*, invalidates any proposal to include these metacercariae in a single group. Although *Neascus*, as shown above, is not a natural group, it is not possible in the present state of our knowledge to split *Neascus* into *Neodiplostomulum* (in part) and *Neascus sensu stricto*, using only metacercarial characters.

(*d*) *Reserve excretory system*

(1) *Development from cercaria*. The reserve excretory system, which is characteristic of the diplostomulum, is foreshadowed in the cercaria by a pair of anterior blind tubules arising from the bladder arms anteriorly (Fig. 17). These tubules,

the primordia of the main lateral vessels of the diplostomulum, grew rapidly once the cercarial body had penetrated a tadpole. At 4 days, each had given rise to a medial branch which joined that from the other side to form the pre-acetabular commissure, from which a median branch arose, and to a posteriorly directed lateral branch (Fig. 24). At this stage the full cercarial spination and the partially emptied penetration glands were present.

At 5 days (Fig. 25), the main lateral, posterior lateral, and anterior median vessels had grown and a posterior median vessel had grown back, dorsal to the holdfast, from the pre-acetabular commissure. At this stage the penetration glands had disappeared and the cercarial spines had been lost except for those in the oral hood.

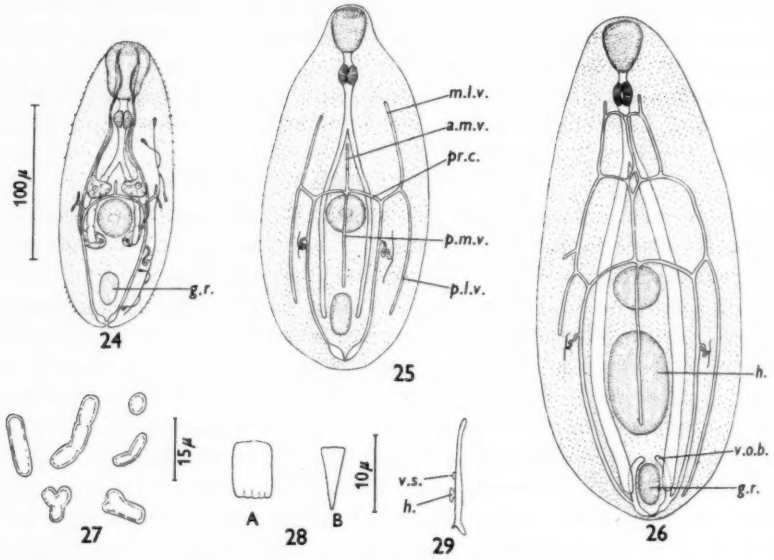

Fig. 24. Developing diplostomulum, at four days, dorsal view.

Fig. 25. Developing diplostomulum, at five days, dorsal view.

Fig. 26. Developing diplostomulum, at seven days, dorsal view.

Fig. 27. Excretory granules of diplostomulum.

Fig. 28. A, scale from ventral surface of diplostomulum anterior to ventral sucker; B, spine from ventral surface posterior to ventral sucker.

Fig. 29. Lateral view of living diplostomulum with holdfast and ventral sucker protracted.

At seven days (Fig. 26), a second commissure had formed at the level of the bifurcation of the gut; this commissure usually formed a simple junction with the anterior median vessel, but occasionally formed a diamond-shaped junction as figured. A third commissure had developed just behind the pharynx, and a pair of ventral outgrowths had arisen from the medial face of the bladder near the origin of the bladder arms. At this stage, neither cercarial nor metacercarial spines were present.

As development proceeded, dendritic branches arose from the main lateral, anterior and posterior median, and posterior lateral vessels. From these branches pockets arose, both terminally and laterally, in which the excretory granules were laid down in a pre-formed matrix. In a few diplostomula, a cross-connexion was present on one side between the anterior median and main lateral vessels.

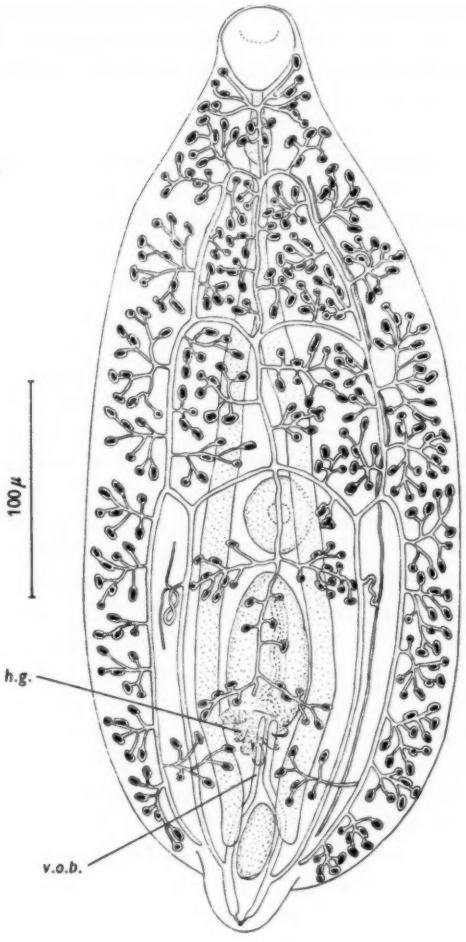

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Fig. 30. Diplostomulum, dorsal view.

By 15 days, the reserve excretory system was fully formed (Fig. 30), and the metacercarial spination had developed. Branches ending in pockets arose from both medial and lateral faces of the main lateral vessels, and each posterior lateral vessel had six to eight lateral branches and a single posterior medial branch. The

ventral outgrowths of the bladder extended forward on either side of the genital rudiment, lay side by side but not joined anterior to the genital rudiment and ended blindly within the substance of the posterior end of the holdfast. The excretory granules varied from cocciform to bacilliform or even Y-shaped (Fig. 27); the larger granules were apparently formed by the fusion of several cocciform granules. The number and relations of the flame-cells were not worked out, beyond noting that there appeared to be three sets of flame cells developed for each flame cell in the cercarial body. The tufts of cilia (lateral flames) in the convolutions of the bladder arm in the cercaria apparently continue to function in the diplostomulum, as they were seen on one occasion.

(2) *Subsequent development.* A stage in the subsequent development of the reserve excretory system was seen in a single immature adult from an experimental infection (Fig. 31). In this specimen, the excretory granules had disappeared and numerous anastomoses had developed between the various vessels of the forebody. Whereas in the diplostomulum there was a pair of ventral outgrowths of the bladder (Fig. 30), in the immature adult a pair of dorsal outgrowths was also present, extending from just in front of the excretory pore to the posterior end of the holdfast. The dorsal and ventral outgrowths were joined by a single opening anteriorly at the level of the union of the two dorsal outgrowths. The united dorsal outgrowths communicated dorsally with the posterior end of the posterior median vessel. The paired ventral outgrowths, which ended at the posterior end of the holdfast in the diplostomulum, had joined broadly between genital rudiment and holdfast, grown forward within the holdfast on either side of the muscular wall of the median sulcus, united anterior to the sulcus, and joined dorsally with the posterior median vessel. The arrangement of vessels in the hindbody of this immature adult is comparable, in broad outline, with that of neasci and of adult strigeoids as described by Hughes (1927) for *Neascus ambloplitis* (= *Uvulifer ambloplitis*), by Hughes (1928) for *Neascus van-cleavei* (= *Posthodiplostomum minimum*), by Bosma (1934) for *Alaria mustelae*, and by van Haitsma (1931*a*) for *Cotylurus flabelliformis*. In all of these species, there are four longitudinal vessels in the hindbody, two dorsal and two ventral, variously joined and subdivided, and apparently variously connected with the vessels of the forebody. In none, however, is there a development of the ventral vessels in the holdfast similar to that described here. In *Neascus ambloplitis* and *N. van-cleavei*, branches from the posterior median vessel are associated with the holdfast.

(3) *Discussion.* The general pattern of the reserve excretory system in the larval group *Diplostomulum* is now well established by the studies of Fraipont (1880, in Braun, 1892) on *Diplostomum volvens* (= *D. spathaceum*); Hughes (1929*b*) on *Diplostomulum scheuringi* and *D. vegrandis*; Hughes (1929*a*) on *D. browni*; Hughes & Berkhout (1929) on *D. gigas* (= *Diplostomum flexicaudum*); Olivier (1940) on *D. micradenum*; Olivier (1942) on the diplostomulum of *Cercaria elodes*; Rees (1955) on *Diplostomulum phoxini* (= *Diplostomum pelmatoides*); Erasmus (1958) on the diplostomulum of *Cercaria X*; Olivier & Cort (1942) on *Diplostomulum emarginatae*; Rankin & Hughes (1937) on *D. ambystomae*; and von Nordmann 1832 and Claparède 1858 on *Tylodelphys clavata* (in Hughes, 1929*a*). The pattern which

emerges from these studies is simpler than that in *Neodiplostomum intermedium*, lacking as it does the post-pharyngeal commissure.

In addition to this commonly found pattern, a simpler one, with a single commissure between the two halves of the system, is described for *Diplostomulum ranae* by Cort & Brackett (1938*a*) and *Pharyngostomum cordatum* by Wallace (1939), and a more complex one for *Alaria canis* and *A. arisaemoides* by Pearson (1956) and *Neodiplostomum texensis* by Chandler (1942). The pattern in *Alaria canis* and *A. arisaemoides* differs from that in *Neodiplostomum intermedium* in having a series of commissures between the posterior lateral vessels and in lacking

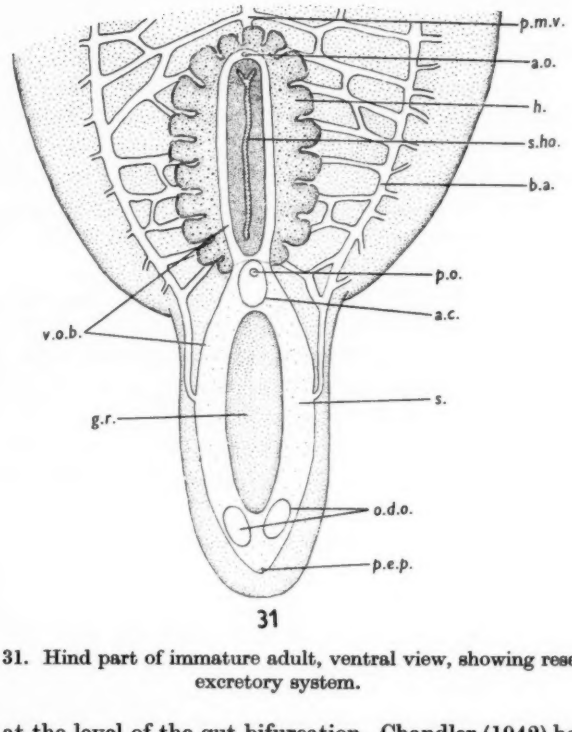

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Fig. 31. Hind part of immature adult, ventral view, showing reserve excretory system.

a commissure at the level of the gut bifurcation. Chandler (1942) has figured but not described the pattern in *N. texensis*, and from the figure it appears that the pattern differs from all other diplostomula in the development of additional commissures between the main vessels, a condition like that in the adult and in the larval group *Neascus*.

Throughout the development of the diplostomulum from the cercaria in *Neodiplostomum intermedium*, those organs (oral and ventral suckers, pharynx, and gut) common to cercaria and diplostomulum remained clearly defined, as found for other diplostomatids by Bosma (1934), Pearson (1956) and Erasmus (1958), and did not disappear as is the case in the holometabolic development of the tetracotyle in the family Strigeidae, as described by Szidat (1924), Wesenberg-

Lund (1934), Olivier (1940), and Ulmer (1957). There is, then, no justification for the statement of Wesenberg-Lund (1934), Hunter & Hunter (1940) and Hunter & Hamilton (1941) that the development of the diplostomatid metacercaria is holometabolic.

(*e*) DISPOSITION IN TADPOLES AND FROGS

In both naturally and experimentally infected tadpoles of *Hyla* sp. diplostomula were found encapsulated, but not encysted, between muscle fibres, mostly in the trunk muscles about the notochord, the only site in light infections, less often in jaw and tail muscles, and rarely in the abdominal wall. In naturally infected frogs of the same species, encapsulated diplostomula were similarly distributed, but were also in the thighs and occasionally in the forelegs. The examination of naturally infected tadpoles at intervals during metamorphosis showed that diplostomula in the body remained encapsulated throughout metamorphosis. On the other hand, diplostomula in the tail were released from their capsules during resorption of the tail; unencapsulated diplostomula were present in the thighs immediately after, but not before, complete resorption of the tail and were subsequently re-encapsulated. These observations suggest that those diplostomula that were carried forward by the resorbing tail migrated into the thighs and became encapsulated a second time.

A similar migration into the limbs at metamorphosis has been described by Cuckler (1949), Hoffman (1955) and Turner (1958) for the diplostomulum of *N. craterum*, by Pearson (1956) for the mesocercariae of *Alaria canis*, and *A. arisaemoides*, and by Pearson (1959*a*) for the mesocercaria of *Strigea elegans*.

Diplostomula of *N. intermedium*, even developing forms a few days old, were always within muscles in tadpoles. Cuckler (1949), on the other hand, found diplostomula of *N. craterum* free in the body cavity of tadpoles, but encapsulated in the hindlegs of frogs. Dubois & Rausch (1950), in their key to the species of *Fibricola*, erroneously state that diplostomula of *N. craterum* became encapsulated in the muscles of tadpoles; they list encapsulation of the diplostomulum in the tadpole as one of several features which separate *N. craterum* and *N. texensis*. I have found (1960) diplostomula of *N. buteonis* free in the body cavity of tadpoles. Chandler (1942) found diplostomula of *N. texensis* free in the body cavity of tadpoles. Ulmer (1955) suggested, on the basis of his and Leigh's (1954) findings, that diplostomula of *N. texensis* may become encapsulated in tadpoles but that this probably takes longer than 2 months, the period of Chandler's (1942) observations. But the observations of Cuckler (1949), Hoffman (1955) and Turner (1958) on *N. craterum*, show that migration into the muscles and subsequent encapsulation do not occur until the tadpole undergoes metamorphosis.

IX. ADULT

The examination of a large series of whole mounts of adults obtained from experimental infections did not reveal any significant differences from the description given by Pearson (1959*b*). The study of serial sections, however, revealed a number of details of the holdfast which were not seen in whole mounts. As these details

are essentially the same in both diplostomulum and adult, they will not be repeated as the holdfast of the diplostomulum has been described earlier in this paper.

The haploid number of chromosomes is 10, with five large and 5 small chromosomes, as determined by aceto-orcein squashes of testes of adult worms. This is, apparently, the first time the chromosome number has been determined for a strigeoid trematode. The haploid number, 10, is common among digenetic trematodes, according to Walton (1959).

Shortly after the paper describing *N. intermedium* was submitted for publication, the journal containing Sandars's (1957) description of *Fibricola sarcophila* was received. A paratype and several experimental adults of *Neodiplostomum intermedium* have been compared directly with material of *N.* (*Fibricola*) *sarcophilus* n.comb., thanks to the kindness of Dr D. F. Sandars. This species, from the marsupial Tasmanian devil, differs from *N. intermedium* in being larger and in having (1) a markedly asymmetric anterior testis which lies toward one side of the body, (2) larger eggs, (3) smaller and more numerous vitelline follicles which, in the hindbody, apparently always extend to the bursal region posteriorly and over the first part of the hindbody dorsally, and (4) forebody with strongly inrolled margins. In *N. intermedium* there are no vitelline follicles in the hindbody dorsally.

In the paper describing *N. intermedium* Pearson (1959*b*) proposed that the genus *Fibricola* Dubois, 1932 be made a subgenus of *Neodiplostomum* Railliet, 1919 and in accordance with this change used the combination *N.* (*Fibricola*) *intermedium* for his new species. The new combinations for the other species in *Fibricola* were listed (Diagram II), but they were not proposed formally and two of these combinations are orthographically incorrect. In this diagram, *N. lucida* should read *N.* (*Fibricola*) *lucidum* n.comb. and *N. cratera* should read *N.* (*Fibricola*) *craterum* n.comb. The other species should read *N.* (*Fibricola*) *minor* n.comb., *N.* (*Fibricola*) *caballeroi* n.comb. and *N.* (*Fibricola*) *texensis* n.comb.

SUMMARY

1. *Neodiplostomum intermedium* Pearson is recorded from four new hosts; as an adult from the water rat, *Hydromys chrysogaster* Geoffroy, and as a metacercaria (diplostomulum), from tadpole and adult of an undescribed tree frog, *Hyla* sp., tadpole of (*Hyla latopalmata* (Günther) *Mixophyes fasciolatus* Günther and frog of an unidentified leptodactylid.

2. The life cycle of *Neodiplostomum intermedium* was followed experimentally; the hosts were: *Pettancylus assimilis* (Petterd), a fresh-water limpet, as first intermediate host; tadpole of *Hyla pearsoni* Copland as second intermediate host; *Hyla caerulea* (Shaw) a tree frog, and *Hemisphaerodon gerrardi* Peters, the pink-tongued skink, as paratenic hosts; and *Rattus assimilis* (Gould) and laboratory rats as definitive hosts.

3. Descriptions are given of the morphology of the miracidium, mother sporocyst, daughter sporocyst, cercaria, and diplostomulum, with special reference to the structure of the miracidium and of the cercarial tail.

4. Observations are given on the embryology of the miracidium, hatching of the egg, transformation of the miracidium into the mother sporocyst with special

reference to the germinal cells, the route and manner of escape of cercariae from the snail host, the development of the diplostomulum with special reference to the reserve excretory system, and the movements of diplostomula during metamorphosis of the tadpole host.

5. The haploid chromosome number is ten, as determined from squashes of testes. One paratype and a series of experimental adults have been compared with and found different from *Neodiplostomum* (*Fibricola*) *sarcophilus* n.comb. The orthography and formal proposing of the names of the species of *Fibricola* transferred to *Neodiplostomum* by Pearson (1959*b*) are corrected.

The writer wishes to thank Dr M. J. Mackerras, Queensland Institute for Medical Research, for generously supplying water rats; Professor J. F. A. Sprent, University of Queensland Veterinary School, for his criticism of the manuscript; Mr K. Webber and his sons for their assistance in catching rats and for permission to collect snails, frogs and tadpoles from their streams; and Mr R. J. Ballantyne for technical assistance. This study was supported by a grant from the Rural Credits Fund of the Commonwealth Bank of Australia.

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KEY TO LETTERING

a.b.t.	anterior blind tubule
a.c.	anterior connexion between dorsal and ventral bladder outgrowths
a.g.	apical gland
a.h.c.	anterior hyaline cell
a.m.v.	anterior median vessel
a.o.	anterior opening between posterior median vessel and ventral bladder outgrowth
b.a.	bladder arm
b.c.	body cavity
b.p.	birth pore
c.	cell on lateral nerve fibre
c.b.	caudal body
c.b.d.c.	cell bodies of dorsal commissure
c.e.t.	caudal excretory tubule
c.f.	dorso-ventral cuticular folds
c.fi.	circular fibre
c.g.	cephalic gland
c.m.f.	circular muscle fibre
c.p.p.	commissure to postero-lateral papilla
c.s.h.	cilium-like, lashing sensory hair
c.v.m.	cell which forms vitelline membrane
d.e.	disintegrating eyespot
d.l.m.b.	dorsal band of striated longitudinal muscle on lateral face
d.n.m.	disintegrating neural mass
d.s.e.	daughter sporocyst embryo
e.	eyespot
e.a.	excretory atrium
e.c.	E, or ectodermal, cell
e.f.	extensors of furcae (dorsal segment of fibres omitted)
e.m.	embryo of miracidium
e.p.	excretory pore
e.pl.	epidermal plate
ey.p.	eyespot pigment
f.c.	flame cell
f.d.c.	fibres of dorsal commissure
f.e.p.	furcal excretory pore
f.e.t.	furcal excretory tubule
f.n.	free nucleus (? of hyaline cell)
g.c.	germinal cell
g.m.	germinal mass
g.r.	genital rudiment
h.	holdfast
h.g.	holdfast gland
i.f.	inter-furcal fibres, flexors of furcae
i.f.f.	inter-facial fibres
l.d.b.	left dorsal band of striated longitudinal muscle fibres (cut away posteriorly)
l.n.f.	lateral longitudinal nerve fibre
l.pa.	lateral papilla
l.pr.	lateral process
m.l.m.	striated longitudinal muscle fibre of median face
m.l.v.	main lateral vessel
m.p.c.	main posterior commissure
m.v.p.	mid-ventral plate of second tier
n.	nuclei on inner face of longitudinal muscle branch, possibly nervous
n.c.f.	nucleus of circular fibre
n.c.m.	nucleus of circular muscle fibre
n.e.p.	nucleus of epidermal plate
n.e.t.	nucleus of excretory tubule
n.g.	nucleus of granular cell associated with excretory tubule
n.m.	neural mass
n.my	nucleus of ? myoblast
n.p.	nucleus of posterior cell to which posterior granular body is attached
n.v.m.	nucleus of vitelline membrane
o.c.g.	opening of cephalic gland
o.d.o.	origin of dorsal outgrowth of bladder
p.	papilla bearing sensory hair
p.a.	prolongation of anterior hyaline cell
p.c.	P cell, or propagatory cell
$p_1c.$	P_1 cell
p.e.p.	position of excretory pore
p.g.b.	posterior granular body
p.h.c.	posterior hyaline cell
p.l.v.	posterior lateral vessel
p.m.v.	posterior median vessel
p.o.	posterior opening between posterior median vessel and dorsal bladder outgrowths
p.p.	postero-lateral papilla
pr.c.	pre-acetabular commissure
r.v.b.	right ventral band of striated longitudinal muscle (right dorsal band omitted)
s.	septum separating dorsal bladder outgrowths from bladder and ventral outgrowths
s.a.h.c.	sulcus in anterior hyaline cell
s.h.	sensory hair
s.ho.	sulcus of holdfast
s.m.l.	submuscular layer
v.	vacuole
v.c.	vitelline cell
v.m.	vitelline membrane
v.o.b.	ventral outgrowth of bladder
v.r.	vitelline remnants
v.s.	ventral sucker
y.	yolk granules
z.	zygote

Parasitology (1961), **51**, 173–179
Printed in Great Britain

Certain aspects of the host-parasite relationship of Nematospiroides dubius (Baylis)

I. Resistance of male and female mice to experimental infections

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(*Received* 12 *March* 1960)

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INTRODUCTION

It is now well known that the male host can have a different susceptibility to a parasitic infection compared with that of a female host. Hunninen (1935) showed that for some days after parturition female mice became more resistant to *Hymenolepis nana* var. *fraterna*. Culbertson (1941) listed the following parasites as being affected by the sex of the host: *Entamoeba histolytica*, *Leishmania*, malarial parasites, *Haemonchus contortus*, *Syngamus trachea*, cysticercoids, *Hymenolepis nana* var. *fraterna* and *Trypanosoma equiperdum*. From the literature it appears that the female host has the greater resistance to parasitic infection, but Whitlock (1937) and Clapham (1939) found the incidence of *Syngamus trachea* higher in the female than in the male partridge. Campbell (1939) and Campbell & Melcher (1940), showed that castration, followed by the administration of oestrogen to male rats, increased their resistance to *Cysticercus crassicollis*, whereas androgens administered to the spayed female seemed to have the opposite effect. However, Stoll (1940) showed that the native resistance of ewes to *Haemonchus contortus* decreased during gestation and lactation. Chandler (1943) and Addis (1946) found that testosterone favoured the growth of *Hymenolepis diminuta* in rats. Todd & Hollingsworth (1952) observed that the male chick harboured a small, but significantly greater, number of *Ascaridia galli* than the female chick did. Ackert & Dewhirst (1950) found that the resistance of chicks to *A. galli* increased to a maximum at about the age of sexual maturity and that injections of diethylstilboestrol increased the resistance of the female chicks. Sadun (1948, 1951) found that the resistance of the male chick was likewise increased by the injection of testosterone, but Todd, Crowdus & Wyant (1951) found that it was not affected by methyltestosterone given in the diet, although the length of the worm increased. Beck & Chandler (1950) and Beck (1952) observed that, when only a single indi-

vidual of *Hymenolepis diminuta* was experimentally established in rats, a higher rate of egg production was reached more quickly in the male than in the female rat; they also found that castration of the male host lowered the rate of egg production, but administration of the homologous sex hormone restored it. Roman (1951) noted during a survey of natural infections of mice with *Aspicularis tetraptera* that 48 % of the males, but only 24 % of the females harboured this nematode. Ehrenford (1957) showed that there is in dogs, naturally infected with *Toxocara canis*, a relationship comparable to this. Haley (1958), observed that the male hamster, an abnormal host of *Nippostrongylus muris*, harboured significantly more individuals of this species than the female did. Mathies (1954, 1959) showed a similar relationship between infections of male and female mice with *Aspicularis tetraptera*; he also found that gonadectomy significantly lowered the worm burden and that oestradiol administered to the male mouse was detrimental to the establishment of heavy infections, while testosterone had little or no effect in either male or female mice. Berg (1953, 1957) showed that injection of testosterone into mice infected with *Schistosoma mansoni* lowered the survival of the parasite, but Robinson (1959) denied any such modification of the survival rate. It is worthy of note that a sex difference to an infection may occur in invertebrate hosts. Thus Burtt (1946) and Ashcroft (1959) found a significantly greater rate of infection with *Trypanosoma cruzi* and *T. rhodensiense* in the male than in the female *Glossina morsitans*.

Because the details of the host-parasite relationship of *Nematospiroides dubius* were unknown, before the work described here began, and because, as Sheffield, Meisenhelder & Thompson (1959) and Lynch & Nelson (1959), have pointed out, this parasite is becoming increasingly important in the screening of anthelminthics, an investigation was undertaken of some aspects of the host-parasite relationship of this species. The life cycle of *N. dubius*, Ehrenford (1954), involves one preparasitic moult before entry to the host through the mouth. The first ecdysis occurs in the duodenum of the mouse as the larva penetrates the wall of the intestine, in which it encysts. Here it moults twice and after 6 days returns to the lumen of the gut as an adult worm. The whole cycle, from egg to egg, takes 18 days.

MATERIALS AND METHODS

All the animals used were from a colony of Swiss strain mice free from helminthes, in which the first oestrous occurs between 30 and 40 days. Mice aged between 10 and 55 days were therefore used to ensure that both sexually mature and sexually immature mice were studied. All the mice were maintained in cages over sawdust, food in pellet form and water being available at all times. Mice which had not been weaned were left with their mothers after they had been infected. All the mice were maintained under the same conditions of light, temperature and humidity.

The original stock strain of *Nematospiroides dubius* (Baylis) was obtained from the Wellcome Research Laboratories, London and was maintained in Swiss strain male mice.

Fresh faeces from infected mice were kept on No. 54 Whatman filter-paper moistened with dechlorinated water and then covered with wet, activated, granulated charcoal (washed in dechlorinated water to remove the dust) in covered dishes, following the methods of Spurlock (1943) and the Wellcome Laboratories of Tropical Medicine, London. The cultures were kept in the dark at 22–24° C. under 100 % relative humidity. Infective larvae appeared in large numbers after 7 days and were isolated by flooding the cultures with dechlorinated water and allowing them to stand for 4 hr., by which time the larvae had migrated from the filter-paper into the water. The suspension of larvae was then decanted and centrifuged at 2000 r.p.m. for 10 min. and the precipitated larvae were resuspended in a small volume of water, which was adjusted so that 0·2–0·3 ml. of the suspension contained the number of larvae required to infect one mouse (estimated by counting the number of larvae in known volumes of the suspension).

Each mouse was weighed and infected by stomach tube with fifty larvae of *N. dubius* in water. After 5 or 10 days the mice were killed by cervical dislocation. The body was then weighed and the gut was removed and the portion between the pyloric sphincter and the anterior end of the caecum was measured and placed in saline. The small intestine from mice infected for 5 days was mounted between two glass plates on the stage of a dissecting microscope and illuminated by reflected light, so that it could be examined over its whole length. The larvae which had penetrated the gut wall were counted and the length of the intestine along which they had encysted was measured.

The intestine from mice infected for 10 days was treated similarly, except that in addition the gut was slit open and the adult parasites were removed to a drop of saline on a slide, where they were counted and sexed. The length of the intestine in which these free worms occurred was also measured.

RESULTS

On the fifth day of the infection forty-eight male mice harboured between 10 and 47 (average 27·48 ± 1·78) cysts. These were found infecting 38·76 (± 6·43) % of the small intestine between the stomach and caecum.

Similarly thirty-four female mice harboured between 6 and 36 (average 20·03 ± 1·56) encysted larvae along 38·3 (± 0·88) % of the small intestine.

Using Students' '*t*' test, the comparisons of these means showed that the worm burden in the male was significantly greater than that in the female mouse ($P = < 0{\cdot}001$), although there was no significant difference in the length of the small intestine infected (see Tables 1 and 2).

By the tenth day of infection the encysted larvae had passed back into the lumen of the intestine as adult parasites. The worm burdens of thirteen male mice then varied from 15 to 42 (average 30·69 ± 2·42) infecting 23·41 (± 4·49) % of the small intestine, while the worm burdens of eleven female mice were between 13 and 35 (average 24·03 ± 1·8) infecting 22·89 (± 6·5) % of the small intestine.

When comparisons were made it was found that the male harboured significantly more parasites than the female mouse ($P = 0{\cdot}01$–$0{\cdot}001$) after an infection of 10

days. There was, however, no significant difference between the lengths of the intestine infected, but, in both the male and female mice, significantly more of the intestine was infected on the fifth day than on the tenth day of infection (P = 0·01–0·001) (see Table 2).

The number of cysts formed by the fifth day of infection, compared with the number of adult parasites in the lumen of the gut on the tenth day, were not significantly different in the male mouse, but there was a significantly larger population of adult worms in the female mouse (P = < 0·001). Thus, by the fifth day of infection, not all of the larvae had formed observable cysts in the female mouse.

Table 1. *Worm burdens in male and female mice infected with* Nematospiroides dubius *for* 5 *and* 10 *days. Infective dose* 50 *larvae in* 0·2–0·3 *ml. of dechlorinated water*

Sex of host. Period of infection (days)	No. of mice used	Average worm burden	't' value	Male parasites		Female parasites
Male mouse (5 days)	48	27·48 ± 1·78	8·66	—		—
Female mouse (5 days)	34	20·03 ± 1·56	1·95	—		—
Male mouse (10 days)	13	30·69 ± 2·42	4·44	15·08 ± 1·38	't' value	15·61 ± 1·43
Female mouse (10 days)	11	24·03 ± 1·8	3·68	13·36 ± 1·01	8·12	11·36 ± 1·04

Table 2. *Average weight of mice used; length of gut from the stomach to caecum; and the differential significance of the length infected in male and female mice*

Sex of host. Period of infection (days)	No. of mice used	Total body weight Before (gm.)	Total body weight After (gm.)	Gut length (cm.)	Percentage gut infected	't' values
Male mouse (5 days)	48	14·91 ± 0·93	18·73 ± 0·89	40·24 ± 1·10	38·76 ± 6·43	
Female mouse (5 days)	34	12·94 ± 1·05	14·42 ± 0·83	32·4 ± 0·57	38·3 ± 0·88	3·42
Male mouse (10 days)	13	11·83 ± 6·1	15·58 ± 1·92	37·71 ± 2·21	23·41 ± 4·49	2·41
Female mouse (10 days)	11	13·25 ± 2·24	16·5 ± 1·59	39·71 ± 2·34	22·89 ± 6·5	

The adult parasites were sexed and it was found that, although male and female worms were recovered in equal numbers from the male mouse, a significantly greater number of male than female parasites was recovered from the female mouse (P = < 0·001) (see Table 1).

DISCUSSION

The parasitic part of the life cycle of *N. dubius* is made up of two major phases; a tissue phase, passed as a larva encysted in the gut wall, and an adult phase, passed in the lumen of the small intestine.

Campbell & Melcher (1940); Sadun (1948, 1951) and Mathies (1959) have already shown that oestrogen stimulates the resistance of the host to the parasite, while testosterone has little or no effect. During its life cycle, therefore, *N. dubius* might be acted on by two resistance mechanisms, both of which are controlled by

oestrogen: first, by an indirect mechanism involving the laying down of connective tissue and the antibody reaction; secondly, the direct mechanism, acting on the adult parasite, of oestrogen carried in the blood and bile.

N. dubius must, during its tissue phase, be open to attack from the antibody reactions of the host. These antibodies may be produced in different quantities in male and female hosts, the production being governed by the respective sex hormone. This could, therefore, account for some of the sex resistance. Weinstein (1939) showed that the oestrogenic hormones possess the ability to increase the amount of circulating antibody to *Escherichia coli* in both male and female rabbits and von Haam and Rosenfeld (1942) observed that the administration of oestrone increased the resistance of both gonadectomized and normal male rabbits to *Pneumonococcus*, testosterone being without effect. While the larva is encysted, oestrogen could also act upon it directly. This might account for the fact that a significantly smaller number of parasites were counted in the female mouse after 5 days of infection than were counted after 10 days. Oestrogen had thus retarded the rate of development of the worm (see Table 1). Also, significantly more male than female adult parasites were recovered from the female mouse ($P = < 0{\cdot}001$). This could also be a consequence of oestrogen acting directly on the parasite within the tissues of the host. No entirely satisfactory explanation can, however, be given as yet for the survival of more male than female nematodes in the female host. It is known that oestrogen also facilitates the laying down of connective tissue. This could be detrimental to the parasite while it is encysted in the intestinal wall, because the host encapsules the worm in a connective tissue sheath, which tends to prevent the escape of the parasite and is more readily laid down in the female than it is in the male host. Asboe-Hansen (1958) states that the injection of oestrogen into certain animals induces an increase in the mucopolysaccharide content, particularly the hyaluronic acid content, of all connective tissues.

Mathies (1959) discusses the importance of bile as a carrier of oestrogen and the effect of this hormone on infections of *Aspicularis tetraptera*, stating that, because there are no tissue phases during the life cycle of *A. tetraptera*, any sex resistance due to the direct action of oestrogen must occur in the intestine, perhaps as a result of the action of oestrogen excreted in the bile. Pearlman *et al.* (1948) found that more oestrogen was excreted in the bile than in the urine of dogs and that a small, but significant, amount was passed in the faeces, but that this appeared to come directly from the blood stream. It is also known that bile acts directly upon parasites, inhibiting their metabolism of sugars. Rothman (1958, 1959) showed that bile salts inhibited the fermentation of glucose in *Hymenolepis diminuta* and *Oochoristica symmetrica* from both rats and hamsters. The dual effect of bile and oestrogen acting directly upon the parasite is probably a governing factor causing the worms to occupy a significantly shorter length of intestine after 10 days than after 5 days ($P = 0{\cdot}02$ or $0{\cdot}01$–$0{\cdot}001$) (the majority of the adult worms migrating to an area lying anterior to the flow of the bile) (see Table 2). It is also known that oestrogen has a direct action on nematodes. Thus Rosen, Dougherty & Bern (1951) found that oestradiol in sterile cultures strikingly reduced the reproduction of *Rhabditis briggsae*, whereas testosterone had a stimulatory effect.

SUMMARY

1. It has been shown that there is a difference between the resistance of male and female mice to infection with *Nematospiroides dubius*.

2. More parasites were harboured, during both the larval and adult parasitic phases, by male mice.

3. These worms were found to occupy a similar relative length of the intestine between the stomach and the caecum in male and female mice infected for either 5 or 10 days.

4. The relative length of the intestine infected on the fifth day was significantly greater than that infected on the tenth day.

This investigation was carried out during the tenure of a Research Studentship from the Department of Scientific and Industrial Research. I should like to thank Professor I. Chester Jones, in whose department the work was done, for the facilities provided and Dr E. T. B. Francis for his helpful and critical supervision.

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Parasitology (1961), **51**, 181–192
With 2 plates and 3 text-figures
Printed in Great Britain

Studies on *Demodex folliculorum* Simon (1842)

I. Life history

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(*Received* 27 *April* 1960)

INTRODUCTION

Hirst (1919), in his classical description of the morphology of *Demodex folliculorum* Simon (1842), has given the stages of its life-cycle as: ovum, larva, protonymph, deutonymph and adult. Fuss (1933, 1935) also demonstrated the various stages of the life-cycle as: ovum, hexapod larva, octopod larva, nymph, adult. Hurst's terminology is that usually employed throughout the order Acarina, and it will be used here. Correspondence between Hirst and Fuss is as follows: ovum = ovum, larva = hexapod larva, protonymph = octopod larva, deutonymph = nymph, adult = adult. Megnin (1880) considered the animal to be viviparous, but Fuss has provided clear evidence that it is oviparous.

The precise course of the life-cycle, however, particularly in respect of the duration and respective habitats of each stage, is not known. The method of dissemination is also unknown though various suggestions have been made. These lacunae in our knowledge are unfortunate, especially as this mite is of importance in certain human diseases. The histological, experimental and cultural work here described was done with the object of filling these gaps in our knowledge.

MATERIAL AND METHODS

(1) *Histological*

Sections of human skin containing *D. folliculorum* were examined and the location and stage of each specimen noted. In order to determine whether or not all stages of the parasite are confined to the skin, large numbers of sections of other human tissues, e.g. lymph nodes, liver, pancreas, gut, were examined. All the sections were 5μ thick and were stained with Harris's haematoxylin and eosin after fixation in formal-saline and embedding in paraffin wax.

(2) In vitro *culture*

Mites used for culture were obtained from follicles of the facial skin of man by the gentle application of a comedone expressor. The mites were removed with a finely drawn glass needle and placed in sebaceous material thinly spread on a coverslip. The sebaceous material used was obtained from hair follicles and uninfected sebaceous cysts and was mixed with small quantities of penicillin and streptomycin to prevent bacterial contamination. A cavity slide was prepared and the

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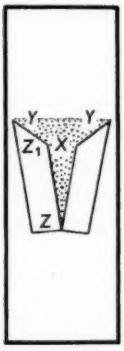
prepared coverslip was placed on it so that the material lay on the undersurface of the coverslip. The preparation was then placed in a blackened petri dish and kept at 37° C. A piece of moist filter-paper was kept in the Petri dish to ensure a high and constant humidity.

(3) *Experimental*

The mites were obtained by method (2) described above, and the experiments listed below were carried out on the larva, protonymph, deutonymph and adult. All experiments were conducted in a darkened room in order to minimize the effect of extraneous light.

Text-fig. 1



Text-fig. 2

Text-fig. 3

(*a*) *Reaction to light*

The mites were placed on a clean slide. Insertion of a piece of opaque material between the condenser of the microscope and the object made it possible to illuminate a portion of the field while the rest of it remained dark. Brightness of illumination was controlled by placing optical filters between the microscope mirror and the light source.

(*b*) *Reaction to gravity*

The microscope was adjusted to the horizontal, so that the slide on which the mites had been placed was vertical.

(*c*) *Reaction to heat*

The mites were placed on a slide put into a boiling tube immersed in a water-bath at the following temperatures (° C): 3, 10, 20, 40, 37, 50.

(*d*) *Reaction to humidity*

A boiling tube was prepared as shown in Text-fig. 1; a perforated metal division was placed 2 in. from the bottom; in the space below this water was placed for the first experiment and $CaCl_2$ for the second. Mites were placed on a clean slide and this was placed in the boiling tube. The tube was tightly stoppered and kept at 37° C.

(*e*) *Stereotaxy*

A slide was prepared as shown in Text-fig. 2. The groove Z–Z_1 varied in width from zero at Z to approximately 150μ at Z_1. The groove was filled with sebaceous material from Z to Y–Y. The mites were placed at X and the preparation treated as for culture.

(*f*) *Feeding*

Sebum and lanolin were spread on a slide as shown in Text-fig. 3. The mites were placed at X. In expt. 1 the sebum was lightly stained with methylene blue, while in Expt. 2, the sebum was left unstained and the lanolin was stained. Staining facilitated observation.

RESULTS

(1) *Histological*

Mites were not seen in any of the other tissues examined, only in skin.

It is convenient to zone the pilo-sebaceous apparatus as shown in Table 1.

The techniques employed in the present work appear to make the ova, larvae and ovigerous females very much more fragile than the other stages. Approximately one-fifth of the total number of mites was thereby rendered unidentifiable

Table 1

Zone	Ovum	Larva	Proto-nymph	Deuto-nymph	Adult male	Adult female	Ovi-gerous female	Unidenti-fied	Total mites in each zone
I. Mouth of follicle	0	4	82	91	10	331	5	123	646
II. Pilo-sebaceous canal	7	31	46	6	2	169	2	71	329
III. Sebacous gland	2	14	9	0	1	27	7	48	113
IV. Middle region of follicle	0	2	1	0	0	19	0	9	31
V. Base of follicle	0	1	0	0	0	6	0	4	11
Total	9	52	138	97	13	552	14	255	1130

by the cutting and processing of the sections. It is therefore probable that an even higher proportion of the fragile stages was damaged, so that comparisons between the number of ova, larvae, and ovigerous females, and those of other stages have not been attempted.

Statistical examination of the remaining data in Table 1 showed that:

(*a*) There were significantly more adult females in all regions than adult males.

(*b*) There were significantly more mites of each stage in zones 1–3 than in zones 4 or 5.

(*c*) Adult females were significantly more frequent in 1 than in 2 and significantly more frequent in 2 than in 3.

Table 2. *Culture* in vitro

(Time of initiation of each stage (T) and duration of each stage (D) in hours.)

Expt. no.	Stage introduced	Ovum		Larva		Proto-nymph		Deuto-numph		Adult		Dead
		T	D	T	D	T	D	T	D	T	D	
1	Adult	—	—	—	—	—	—	—	—	0	56	56
	Progeny	Not seen		70	38	108	11	—	—	—	—	119
2	Adult	—	—	—	—	—	—	—	—	0	120	120
	Progeny	Not seen		64	38	102	146	—	—	—	—	146
3	Adult	—	—	—	—	—	—	—	—	0	120	120
	Progeny	—	—	66	36	102	42	—	—	—	—	144
4	Adult	—	—	—	—	—	—	—	—	0	108	108
	Progeny	—	—	67	6	—	—	—	—	—	—	73
5	Adult (female)	—	—	—	—	—	—	—	—	0	92	92
6	Adult (female)	—	—	—	—	—	—	—	—	0	76	76
7	Adult (female)	—	—	—	—		—	—	—	0	45	45
8	Adult (female)	—	—	—	—	—	—	—	—	0	36	36
9	Adult (female)	—	—	—	—	—	—	—	—	0	16	16
10	Adult (female)	—	—	—	—	—	—	—	—	0	70	70
11	Adult (male)	—	—	—	—	—	—	—	—	0	59	59
12	Larva	—	—	0	36	36	—	—	—	—	—	72
13	Larva	—	—	0	26	26	—	—	—	—	—	52
14	Larva	—	—	0	18	40	—	—	—	—	—	58
15	Protonymph	—	—	—	—	0	48	44	—	—	—	92
16	Protonymph	—	—	—	—	0	29	31	—	—	—	60
17	Protonymph	—	—	—	—	0	70	62	132	4	—	136
18	Protonymph	—	—	—	—	0	33	63	96	13	—	109
19	Deutonymph	—	—	—	—	—	—	0	13	13	96	109
20	Deutonymph	—	—	—	—	—	—	0	26	26	120	146
21	Deutonymph	—	—	—	—	—	—	0	40	40	84	124
22	Deutonymph	—	—	—	—	—	—	0	14	14	96	110
23	Deutonymph	—	—	—	—	—	—	0	42	42	96	138

Observations at least every 12 hr. Error ± 12 hr.

(*d*) There were significantly more adults in 1 than in 2 or 3.

(*e*) In the follicles there were significantly more adults than deutonymphs or protonymphs.

(*f*) In the follicles there were significantly more protonymphs than deutonymphs.

(*g*) The proportion of deutonymphs in 1 is significantly greater than the proportion of adult females or protonymphs in this region.

(*h*) There were significantly more protonymphs in 1 than elsewhere.

(*i*) Larvae were significantly more frequent in 2 than elsewhere, and more frequent in 3 than in 1.

(*j*) There were significantly more ova in 3 than elsewhere.

A random sample of infested sections, such as that which provides the data given in Table 1, may be taken as representing the status of a single generation within the follicles. Statistical analysis, therefore, gives indications as to the relative durations of the various stages within the follicles.

(2) In vitro *culture*

Complete larval, protonymph and deutonymph stages are represented. Although there are no data about the entire duration of other stages, some figures can be given:

Ovigerous female and ovum	Minimum 70 hr.
Larva	Maximum 64 hr.
Protonymph	Approx. 36 hr.
Deutonymph	Approx. 72 hr.
Adult female	Minimum 120 hr.
Adult male	Minimum 59 hr.

Adult females alone were introduced into culture in Exps. 1–4. In each experiment, larvae appeared in the culture after an interval of time. The female must therefore have contained eggs when they were put into the culture. The shortest period before the appearance of the larva must have been the maximum time between oviposition and the hatching of the egg.

Table 3. *Conditions of mites obtained from follicles*

Stage	Alive	Dead	Total
Ovum	0	0	0
Larva	13	5	18
Protonymph	48	6	54
Deutonymph	52	6	59
Adult	2	3	5
Adult	115	136	251
Total	230	156	386

Ovigerous females lived for 120 hr., during which time the ovum was deposited. The female, therefore, lives for at least 120 hr. after copulation.

The proportion of dead adults is significantly greater than that of other stages. Mites removed from follicles by expression probably occur in regions 1 and 2. Of these, approximately 10% of the adults were dead. It would appear, therefore, that approximately 50% of the adults in regions 1 and 2 are dead.

(3) *Experimental*

(*a*) *Reaction to light*

Table 4. *Reaction of motile stages to light*

Stage	No. of observations	Dim			Bright		
		+	−	No reaction	+	−	No reaction
Adult (female)	5	0	5	0	0	5	0
Adult (male)	1	0	0	1	0	1*	0
Deutonymph	3	0*	0*	3	0	3	0
Protonymph	3	0	3	0	0	3	0
Larva	2	0	2	0	0	2	0

* No marked reaction.

(*b*) *Reaction to gravity*

All stages remain still or move randomly.

(*c*) *Reaction to heat*

Table 5. *Reaction of motile stages to heat*

Stage and no.	Temperature (° C.)	No. alive after various time intervals				
		15 min.	30 min.	1 hr.	3 hr.	6 hr.
Adult (5)	0	0	0	0	0	0
	10	5	2	0	0	0
	20	5	5	5	5	5
	30	5	5	5	5	5
	37	5	5	5	5	5
	50	2	0	0	0	0
Deutonymph (3)	0	0	0	0	0	0
	10	3	3	3	2	0
	20	3	3	3	3	3
	30	3	3	3	3	3
	37	3	3	3	3	3
	50	3	2	0	0	0
Protonymph (4)	0	0	0	0	0	0
	10	4	0	0	0	0
	20	4	4	4	4	4
	30	4	4	4	4	4
	37	4	4	4	4	4
	50	4	3	0	0	0
Larva (2)	0	0	0	0	0	0
	10	1	0	0	0	0
	20	2	1	0	0	0
	30	2	2	2	2	1
	37	2	2	2	2	2
	50	0	0	0	0	0

(*d*) *Reaction to humidity*

Table 6. *Tolerance of motile stages to humidity* (*temperature constant*)

Stage and no.	Condition	Number alive after various time intervals: ½ hr.	1 hr.	3 hr.	6 hr.
Adult (5)	Wet	5	5	5	5
	Dry	5	5	3	0
Deutonymph (2)	Wet	2	2	2	2
	Dry	2	2	2	1
Protonymph (2)	Wet	2	2	2	2
	Dry	2	1	0	0
Larva (2)	Wet	3	2	2	2
	Dry	2	0	0	0

(*e*) *Stereotaxy*

In all the experiments five mites were used—either five living mites of the appropriate stage, or as many living mites of the stage under examination as were available, together with sufficient dead adult females to make the total number five. When dead adult females were used, these were placed near *Z*. It is possible that in such circumstances there is a chemotaxic effect and the results must be accepted with this reservation.

Table 7. *Stereotaxy of motile stages* (see Fig. 2)

Stage and no.	Position occupied	Time (hr.): 2	4	6	8	10	12	14	24	26	28	30	32	34	36	48
Adult (female) (5)	*Z*	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5
	Z_1	.	1	1	.	.	.	1	.	.	.	.	.	.	.	.
	Z_1–*YY*	1	.	.	1	1	1	.	.	.	.	.	.	.	.	.
Adult (male) (1)	*Z*	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.
	Z_1	1	.	1	1	.	.	.	.	1	1	.	.	.	.	.
	Z_1–*YY*	.	1	.	.	.	.	.	.	.	.	1	1	1	1	1
Deutonymph (2)	*Z*	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2
	Z_1	1	1	.	.	.	.	.	.	.	.	.	1	1	.	.
	Z_1–*YY*	1	1	2	2	2	2	2	2	2	2	2	1	1	.	.
Protonymph (2)	*Z*	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2
	Z_1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
	Z_1–*YY*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Larva (2)	*Z*	.	.	2	.	.	.	.	.	.	1	.	.	.	.	.
	Z_1	2	2	.	2	2	2	2	2	2	1	2	2	2	Ecdysis	
	Z_1–*YY*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

(*f*) *Feeding*

Table 8. *Distribution between lanolin and sebum*

	Expt. 1			Expt. 2		
	Restricted to			Restricted to		
Stage	Lanolin	Sebum	Random movement	Lanolin	Sebum	Random movement
Deutonymph	0	0	4	0	0	4
Protonymph	0	3	0	0	3	0
Larva	0	2	0	0	2	0
Adult (female)	0	6	3	0	6	3
Adult (male)	0	0	1	0	0	1

The experimental results for each stage may be summarized:

Larva
- Negative phototaxy
- Positive stereotaxy
- Low tolerance to heat
- Low tolerance to desiccation
- Continuous feeding

Protonymph
- Negative phototaxy
- Positive stereotaxy
- Low tolerance to heat
- Low tolerance to desiccation

Deutonymph
- Negative phototaxy in bright light, no reaction in dim light
- Negative stereotaxy at first becoming positive after approximately 30 hr.
- Greater tolerance to heat than other stages
- Greater tolerance to desiccation than other stages
- Does not feed

Adult (female)
- Negative phototaxy
- Positive stereotaxy
- Lower tolerance to heat than deutonymph, greater tolerance than other stages
- Feeds intermittently

Adult (male)
- Negative phototaxy in bright light, no reaction to dim light
- Intermittently positively and negatively stereotaxic
- Feeds rarely

DISCUSSION

The results of the histological work show the locations of the different stages within the follicle and also the relative durations of some of the stages. The extent of the movements of the mite throughout its life may be deduced from these results as follows:

The disparity between the numbers of adult males and females could be interpreted in three ways:

(i) More females develop than males.

(ii) The life of the male is very much shorter than that of the female.

(iii) The male spends only part of its life in the follicle.

There is no evidence in support of (i) and this would appear most unlikely. In the absence of further evidence it is not possible to determine the relative validity of (ii) and (iii); it is possible that they are both true in part. If (ii) alone is true the length of life of the male can be only 0·02 of the length of life of the female, according to the general formula:

$$\frac{N_1}{N_2} = \frac{D_1}{D_2}$$

where N_1 = no. of stage 1, N_2 = no. of stage 2, D_1 = duration of stage 1, D_2 = duration of stage 2.

Applying the same formula, we can deduce the relative duration of the other stages, e.g.:

$$\text{Life-span of the adult female} = \frac{566}{138} \times 2^* = 8{\cdot}35 \text{ of that of the protonymph,}$$

$$\text{Life-span of the protonymph} = \frac{139}{97} = 1{\cdot}422 \text{ of that of the deutonymph.}$$

Each stage is assumed to be in the pilo-sebaceous apparatus throughout its life.

This formula may also be used to estimate the relative lengths of time during which a stage inhabits different regions of the follicle. It gives the following figures, which are expressed at decimal fractions of unity:

Adult	I. 0·628	II. 0·3208	III. 0·0432
Gravid	I. 0·3571	II. 0·1429	III. 0·5000
Deutonymph	I. 0·938	II. 0·062	III. 0·000
Protonymph	I. 0·5984	II. 0·3358	III. 0·0658
Larva	I. 0·0766	II. 0·6377	III. 0·2857

The data from *in vitro* culture experiments give the actual duration of some of the stages, so that, by a synthesis of these and the histological data, the movements of the mite can be correlated with time.

Discrepancies occur between the histological results and data from *in vitro* culture. Histological evidence shows that the protonymph is in the follicle approximately one and a half times as long as the deutonymph, whereas cultural experiments show that the life of the protonymph is only one and one-sixth as long as that of the deutonymph. This discrepancy can be accounted for by assuming that the deutonymph is only in the follicle for about four-fifths of its life. The deutonymph is usually found in the follicle opening, so that it would seem possible that part of its life is spent on the skin surface. The experimental evidence shows that the deutonymph and adult male can tolerate variable conditions better than the

* A factor of 2 is allowed on the assumption that there are equal numbers of male and female adults.

other stages can and it may therefore be concluded that the deutonymph is the distributive phase, which distributes the species, not only to other follicles of the host on which it occurs, but also to the skin and follicles of other individual hosts.

A similar, but even more marked, discrepancy occurs between the histological and *in vitro* culture evidence relating to the adult male. Though the histological evidence indicates that the length of life of the male is about one-fifteenth of that of the female (cf. p. 189), the cultural evidence shows that it may be half as long. The male, like the deutonymph, is fairly tolerant of variable conditions and it is only found in the opening of the follicle. It may be presumed, therefore, that the greater part of its life is spent on the skin surface, and that the follicle is entered only occasionally for feeding, copulation occurring if there are females in the mouth of the follicle.

The life-cycle may, therefore, be reconstructed as follows: Copulation occurs in the opening of the follicle. The gravid female then makes its way into the sebaceous gland, in which the egg is deposited. The larva hatches up to 60 hr. after oviposition, the interval between copulation and oviposition being approximately 12 hr. The larva feeds continuously and moults after a life of approximately 40 hr, giving origin to the protonymph. This occurs in the pilo-sebaceous canal. The protonymph feeds continuously and is at the same time carried to the opening of the follicle by the flow of sebum. The legs of the protonymph are, in comparison with those of the adult, feebly developed (Hirst, 1919), so that the protonymph can offer little effective resistance to this movement. The protonymph after a life of approximately 72 hr. gives origin to the deutonymph. After a short interval, during which it feeds, the deutonymph crawls on to the skin surface. It may move randomly over the surface for as long as 36 hr., but more usually does this for about 12 hr. and it probably moves over the skin surface only in darkness or dim light. The deutonymph then enters a follicle and moults after a life of 60 hr. to become adult. The female remains in the mouth of the follicle until copulation occurs. The number of eggs produced is not known, but because they are of large size and because only a few larvae are produced in culture, it would appear that the eggs are few. The adult female, having accomplished oviposition, moves back to the mouth of the follicle where, after a life of approximately 120 hr., it dies. It has been shown that about half of the mites in the mouth of the follicle are dead. Dead mites therefore tend to block up the follicular opening and to discourage fresh infestations. This, from the parasite's point of view, may well tend to reduce the chances of uneconomic infestation of individual follicles.

An approximate estimation may thus be made as to the length of the life cycle of the female: ovum 60 hr., larva 36 hr., protonymph 72 hr., deutonymph 60 hr., adult female 120 hr., total 348 hr. or 14½ days. It must be emphasized that these figures are based on the evidence of *in vitro* culture, and that for this reason it is possible that they deviate somewhat from values based on *in vitro* studies. It would, however, seem reasonable to regard them as being of the right order.

No evidence has been found to suggest that the mite ever occurs in tissues other than the hair follicles and their associated sebaceous glands. El-Gindy (1952) has found the closely related species *D. canis* in the superficial lymph nodes of the dog.

this species being usually found in the sebaceous glands and hair follicles of the dog. Demodectic mange is a serious disease to canines which is complicated by the tendency of the dogs to scratch the infected areas and to cause widespread wounds in this way. It is possible that the mites observed by El-Gindy gained entrance through wounds thus caused into the lymph vessels and by way of these into the lymph nodes. There is no evidence that *D. folliculorum* ever does this. The evidence we have shows that the mite is in all its stages a parasite of the pilo-sebaceous apparatus only and there is no evidence to support the view that it is disseminated through the vascular system or that the human infant may be infected *in utero*.

SUMMARY

1. Histological data are given about the location and frequency of the different stages of the life history of *D. folliculorum* in the pilo-sebaceous apparatus of man. These data are examined statistically and the relative durations of each stage and their movements in the follicle are deduced from them.

2. A method of *in vitro* culture is described and data are given about the longevity of the various stages of the life history.

3. Experiments on the behaviour of the different motile stages of the mite are described. It is concluded that the deutonymph is the distributive stage, and that distribution occurs over the skin surface.

4. The life history is reconstructed by a synthesis of the evidence presented. The life-cycle lasts approximately 14½ days, the life span of each stage of it being: ovum 60 hr., larva 36 hr., protonymph 72 hr., deutonymph 60 hr., adult 120 hr. Interval between copulation and oviposition 12 hr.

This work was largely carried out in the Department of Pathology of the Institute of Dermatology, London, and I wish to thank the Director of Pathology, Dr J. O. Oliver, for making available to me the facilities of his department, and for his advice and interest during the progress of the work. The photographs were prepared by Mr R. H. Lunnan of the Photographic Department of the Institute of Dermatology. I am indebted to the Dean of the Institute of Dermatology for permission to publish the photographs.

I am grateful to Mr T. E. Hughes of the Department of Zoology, Birkbeck College, University of London, for his advice at all times, and to Miss Hilda Davies of the Department of Statistics, University of Sheffield, for help with statistical methods and to Mr W. Moseley, who prepared the text figures.

Finally, I wish to express my thanks to Professor I. Chester Jones and Dr E. T. B. Francis of the Department of Zoology, University of Sheffield, for reading the manuscript and for their help in its preparation.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. *Demodex folliculorum*. V.S. skin showing ovigerous female in a sebaceous gland. (× 462.)

Fig. 2. *D. folliculorum*. V.S. skin showing ovum and fragments of two adult females in a pilo-sebaceous canal. (× 220.)

Fig. 3. *D. folliculorum*. V.S. skin showing larva in a pilo-sebaceous canal. (× 220.)

Fig. 4. *D. folliculorum*. V.S. skin showing protonymph in the mouth of a follicle. (× 220.)

PLATE 2

Fig. 1. Ecdysis, protonymph to deutonymph, from *in vitro* culture. (× 462.)

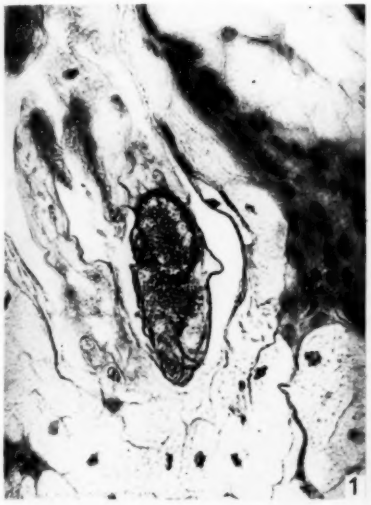
Fig. 2. Ecdysis. V.S. skin showing deutonymph to adult in the mouth of a follicle. (× 220.)

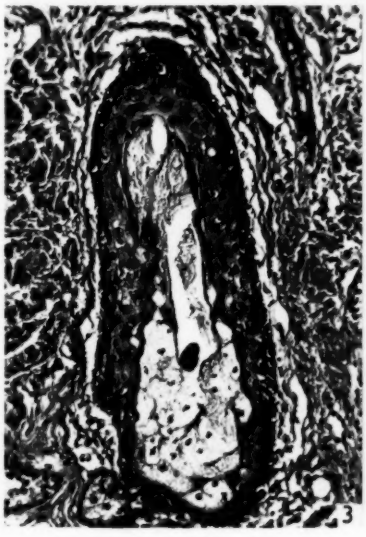
Fig. 3. Ecdysis, deutonymph to adult, from *in vitro* culture. (× 479.)

Fig. 4. V.S. skin showing adult female in a pilo-sebaceous canal. (× 220.)

Fig. 5. V.S. skin showing adult male in the mouth of a follicle, penis indicated by arrow. (× 220.)

Fig. 6. V.S. skin showing dead adult females in the mouth of a follicle; the follicle is shown in transverse section. (× 160.)





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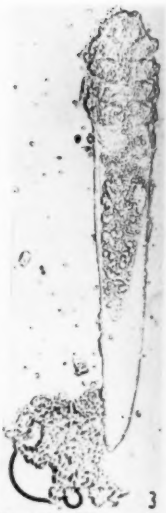
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Parasitology (1961), **51**, 193–226
With 4 plates and 39 text-figures
Printed in Great Britain

Studies on the Functional morphology of the Scolex and of the Genitalia in *Echinobothrium brachysoma* Pintner and *E. affine* Diesing from *Raja clavata* L.

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(*Received* 30 *May*, 1960)

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ECHINOBOTHRIUM AFFINE Diesing

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INTRODUCTION

The genus *Echinobothrium* was established by van Beneden (1849) with *E. typus* from the spiral valve of *Raja clavata* L. as type species. There are now eight known species and two known larval forms. Two species, namely, *E. brachysoma* Pintner and *E. affine* Diesing both from *Raja clavata* off the coast of Britain were given to me in 1957 and 1958 by Dr H. H. Williams, then of this department, to whom I am most grateful. There is no difficulty in the identification of *E. affine* but, owing to some confusion in early descriptions of *E. typus*, it is a little difficult to separate this species from *E. brachysoma*.

E. typus was described by van Beneden (1849) as having two groups of nine large hooks on the rostellum. Later (1861) he stated that there were from nine to sixteen in each group and in one figure draws eleven and in another fifteen. More than one species, therefore, seems to have been involved. *E. typus* was later mentioned briefly by Olsson (1866–7), van Beneden (1871) when he recorded it from *Trygon pastinaca* (L.) (=*Dasyatis pastinaca* (L.)), de Beauchamp (1905) from *Raja punctata* Holb. (=*R. clavata* L.), Southwell (1925) from *R. asterias* Rondel (=*R. montagui* Fowler) and *R. punctata* Holb. Wagener 1854 included in this species a form which Leuckart & Pagenstecher (1858) recognized as being different and which Diesing (1863) named *E. affine*, recording it from *Raja aspera* Flem. (=*R. fullonica* L.), *R. radula* Thompson (=*R. circularis* Couch) and *R. clavata* L.

Pintner (1889) revised the genus and added two more species, *E. musteli* from *Mustelus laevis* Blain (=*Mustelus mustelus* (L.)) and *E. brachysoma* from *Raja batis* L. He included a key for the identification of the now four known species separating them on, among other features, the number of large hooks on the rostellum. *E. typus*, he stated, has seven large hooks in each group, *E. brachysoma* 9, *E. affine* 11 and *E. musteli* 15. This differentiation seems to have been accepted. Ruszkowski (1927) also found seven large hooks in each group in *E. typus* and Joyeux and Baer (1936) gave the same numbers for the four species, which have been recorded only from seas in Europe.

The specimens of *E. brachysoma* described in the present paper have two groups each of nine apical hooks as originally described by van Beneden (1849) for *E. typus*. It is, however, a very much smaller worm, the dimensions agreeing with those given by Pintner for *E. brachysoma*. Pintner recorded *E. brachysoma* from *Raja batis*, L. I have found it to occur in *R. clavata*, L.

Since Pintner revised the genus four other species have been described. Two, namely, *E. rhinoptera* Shipley & Hornell (1906) from *Rhinoptera javanica* Müll & Henle and *E. longicolle* Southwell (1925) from *Trygon kuhli* occur off the coast of Ceylon. *E. raji* Heller (1949) was described from *Raja scabrata* in Canada and *E. Mathiasi* Euzet (1951) from *Leiobatis aquila* L. (=*Myliobatis aquila* (L.)) in the Mediterranean.

Two larval forms are known, *E. levicolle* Lespès (1857) encysted in the liver of *Nassa reticulata* Forbes and Hanley (=*Nassarius reticulatus* (L.)) which Pintner (1889) considers to be the larval stage of *E. musteli*, and *E. Benedeni* Ruszkowsky (1927) encysted in *Hippolyte varians* Leach.

In the following pages a detailed description of *E. brachysoma* is given involving all the systems and with emphasis on the functional morphology of the scolex. It is compared with Pintner's brief account of the same species and with descriptions of *E. typus*. It is also compared in general terms with *E. affine* and a detailed account of the genitalia of the latter species is given.

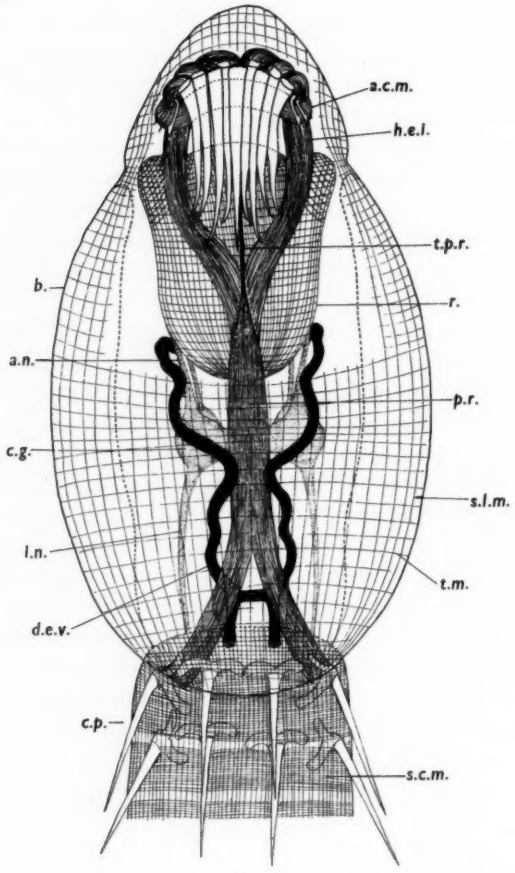
Echinobothrium brachysoma Pintner

Echinobothrium brachysoma occurs in the spiral valve of *Raja clavata* at Plymouth. Specimens were collected by Dr H. H. Williams from fishes brought into the laboratory between the dates 17 August 1958 and 15 September 1958. Some specimens were removed and fixed, large portions of the wall of the spiral valve with worms *in situ* were also fixed and 'squash' preparations of individual worms were made. These latter proved to be most useful. Worms were placed between two slides, compressed just to bursting point and the slides bound together with cotton. The whole was then immersed in fixative 5%, formaldehyde or Bouin's fluid. When fixed *in situ* the worms can be seen protruding from the tubular crypts in the wall of the spiral valve (Pl. 1, fig. 2). They are extremely small and are white except for the last proglottid which is marked by a dark brown patch. Examined with a lens the mucosa in a heavy infestation is speckled with dark dots each of which is a terminal proglottid containing eggs with brown capsules. Some worms were dissected out from the mucosa after fixation, usually with the wall of the crypt in which they were embedded still covering the scolex like the finger of a glove (Pl. 2, figs. 1, 2). These and other entire specimens were stained with Ehrlich's haematoxylin, Gower's carmine and malachite green, acetocarmine, or celestin blue. In the case of the 'squash' preparations (Pl. 3, figs. 3–6) staining and dehydration was carried out while the specimens were still tied between slides, the operation taking about 2 weeks. Serial sections of the worms have been cut 5–7 μ in thickness in three planes and horizontal and vertical sections of the wall of the spiral valve with the worms *in situ*. Sections were stained with Heidenhain's azan of trioxyhaematin. All measurements have been made from fixed material.

EXTERNAL FEATURES

The entire worm (Pl. 3, fig. 1) consists of a scolex and a strobila of up to twelve proglottides only the last of which is gravid. It measures 1·661–2·713 mm. in length. The maximum breadth, in the gravid proglottid, is 0·168–0·223 mm. The scolex measures 0·532–0·597 mm. in length and consists of a head proper and a cephalic peduncle (Text-figs. 1–4). The head proper measures 0·197–0·253 mm. in length and the cephalic peduncle 0·264–0·373 mm. The head bears a dorsal and a ventral flattened oval bothridium which are attached almost throughout their length but are not demarcated from the underlying parenchyma (Text-figs. 9–13). The outline of the head proper and the bothridia varies according to the state of expansion or contraction and to the degree of protrusion of the rostellum. At rest, seen from the dorsal or ventral side it is oval (Text-fig. 1), the bothridium overlapping the cephalic peduncle (Pl. 1, fig. 6). The anterior end of the scolex in this

condition is bluntly rounded (Text-figs. 1–3). When the rostellum is protruded the head becomes shorter, broader and more square in outline (Text-fig. 4) with the anterior extremity flattened or slightly concave. When *in situ* in the tubular crypts in the intestine of the host the bothridia follow the contour of the head, curving round so that the dorsal and ventral bothridia almost meet laterally



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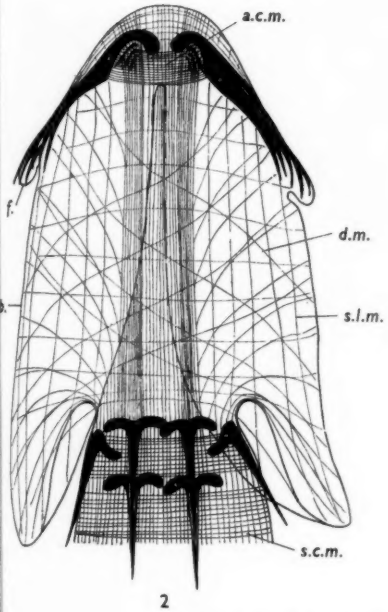
Text-fig. 1. *Echinobothrium brachysoma* Pintner. Scolex (head proper), dorsal view, showing part of musculature, nervous and excretory systems. Apical hooks in resting state.

(Text-figs. 2, 3, 9–13; Pl. 1, figs. 3, 6). The outer exposed surface of each bothridium, therefore, becomes convex and the free lateral portions concave or flattened on their adjacent surfaces (Text-figs. 9–13). The bothridia measure 0·220–0·305 mm. in length with a maximum breadth of 0·144 mm. In this region the width of the scolex itself is 0·073 mm., about half that of the bothridia. At the anterior end the latter pass insensibly into the scolex dorsally and ventrally (Text-fig. 1) and meet

laterally (Text-figs. 2–4). From the widest region the bothridia narrow gradually, posteriorly, to a smooth rounded margin with no evidence of subdivision. The depth of the lateral free portion is about 0·014 mm. The face of each bothridium is unarmed but very tiny spines occur on their adjacent surfaces from a level just behind the rostellum to the posterior end (Text-figs. 11–13). In the region of maximum breadth the depth of the head plus the bothridia is 0·097 mm. More anteriorly the depth is 0·141 mm. and posteriorly that of the head only, just behind the attachment of the bothridia, is 0·08 mm. The area of attachment of the bothridium to the scolex is widest anteriorly where it equals the width of the head



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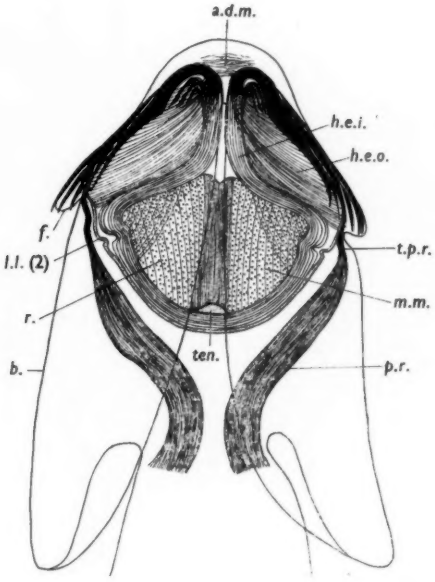

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Text-figs. 2–3. *Echinobothrium brachysoma* Pintner

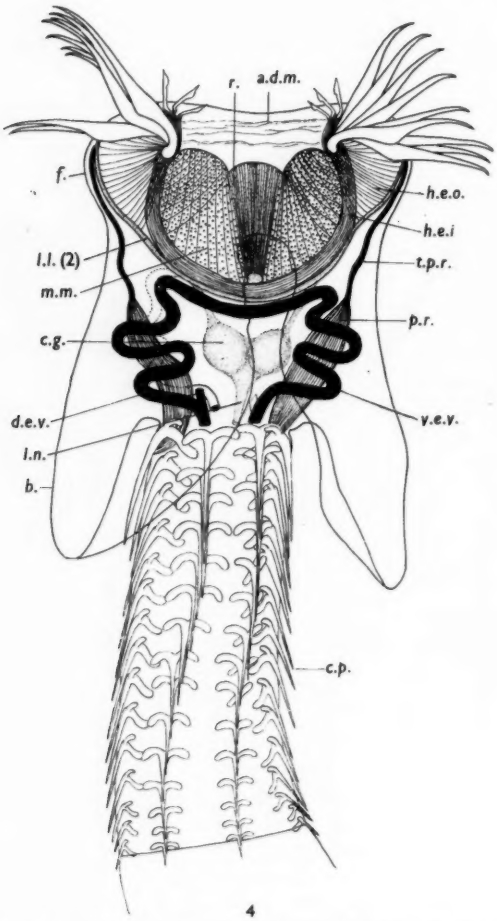
Text-fig. 2. Scolex (head proper), lateral view, showing part of musculature.

Text-fig. 3. Scolex (head proper), lateral view, showing musculature of rostellum and apical hooks. Hooks in resting state.

(Text-fig. 9). It then narrows gradually posteriorly (Text-figs. 9–13). The head itself is fairly uniform in transverse diameter throughout (Text-fig. 1) but the dorso-ventral diameter is greater than the transverse, anteriorly, where it follows the outline of the dorso-ventrally elongated rostellum (Text-fig. 9; Pl. 1, figs. 3–5).

Embedded in the anterior end of the head is a muscular rostellum 0·109 mm. in length and just anterior to the rostellum is a dorsal and a ventral group of hooks (Text-figs. 1, 3, 4; Pl. 1, fig. 4; Pl. 2, figs. 1, 2) lying immediately in front of the bothridia. Each group consists of nine large hooks in two rows with three or occasionally four small hooks on either side (Text-figs. 1, 5*a*, 6). The nine large

hooks are arranged in a constant pattern. There is a posterior row of six the roots of which touch one another and an anterior row of three immediately in front of the central region of the posterior row (Text-fig. 5*a*). In the resting state the hooks lie at an angle of 45° with the longitudinal axis of the scolex, the points directed



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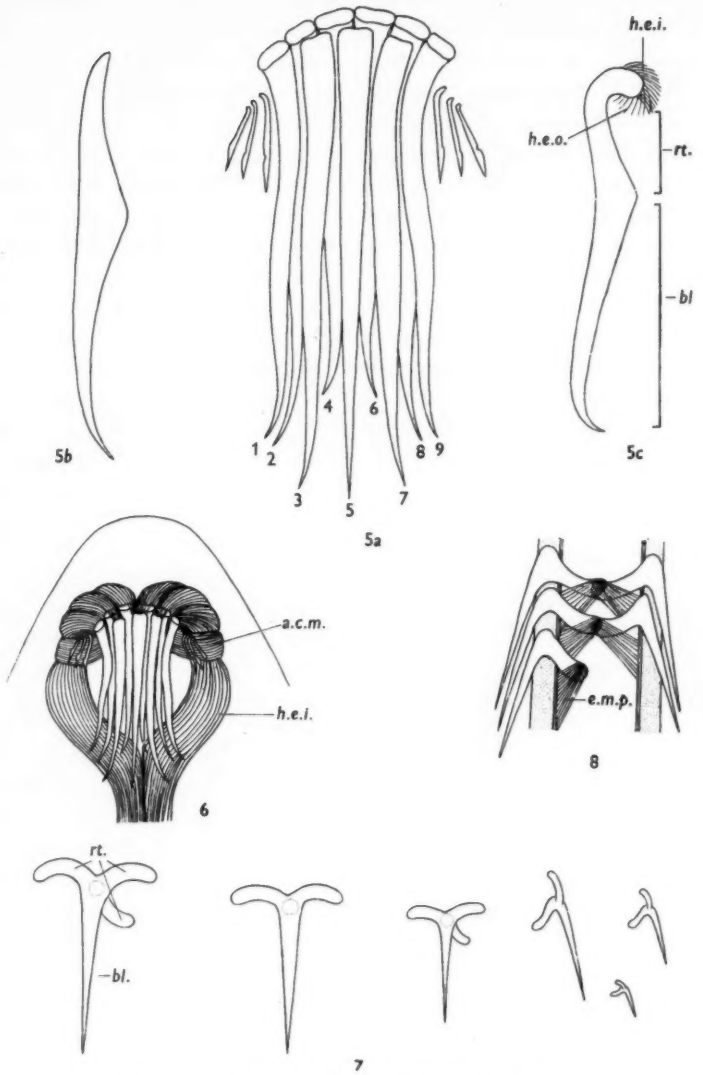
Text-fig. 4. *Echinobothrium brachysoma* Pintner. Scolex, lateral view, showing musculature of rostellum and apical hooks. Hooks raised. Part of nervous and excretory systems shown.

backwards (Text-figs. 2, 3). When in this position there is a transverse fold of the body wall just below their apices. The hooks can be raised through an angle of 95° or more and in this case the fold becomes a lobe covering the outer hook elevator muscles (Text-fig. 4). The hooks vary slightly in length. The three hooks of the anterior row measure, respectively, 0·073, 0·076 and 0·073 mm. Those of the posterior row 0·064, 0·067, 0·066, 0·066, 0·067 and 0·064 mm. The three hooks of



Text-figs. 5–8. *Echinobothrium brachysoma* Pintner

Text-fig. 5*a*. Group of apical hooks, three small hooks on either side.

Text-fig. 5*b*. One hook from outer row, in profile.

Text-fig. 5*c*. One hook from inner row, in profile.

Text-fig. 6. Inner elevator muscles of hooks and part of anterior circular muscle band.

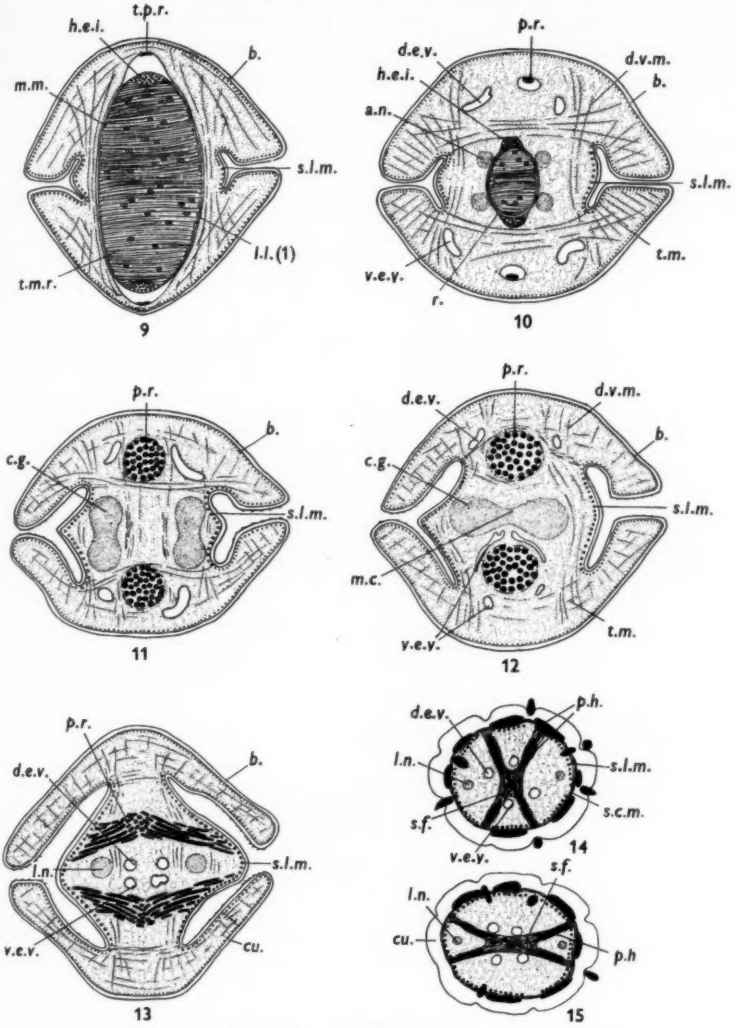
Text-fig. 7. Series of hooks from the anterior to the posterior end of the peduncle.

Text-fig. 8. Longitudinal section through peduncle showing elevator muscles of the peduncle hooks.

the anterior row, therefore, project further back than the six of the posterior row (Text-fig. 5*a*), their apices alternating with the two central ones of the posterior row. Considering all nine hooks together, hook 5, the central one, is the longest, hooks 3 and 7 the next longest, followed by 2 and 8, 4 and 6, 1 and 9. Due to the arrangement of the hooks in an arc, hooks 4 and 6 appear to be the shortest. The hooks of the two rows are slightly different in shape. Those of the posterior row (Text-fig. 5*c*) have a curved blade which is very distinctive in side view. On the outer side the hook describes a double curve, the pointed apex finally turning inwards. The hook is broadest at about one-third of its length, equivalent to the 'guard' of a taenioid hook, from where it narrows gradually to the apex. The 'handle' of the hook is strongly curved. The root, that is the proximal third, is embedded in the scolex, the blade being free. The hooks of the anterior row (Text-fig. 5*c*) have, essentially, the same shape but lack the curved 'handle'. The three or occasionally four small hooks on either side decrease progressively in size towards the outside, measuring 0·020–0·014 mm. in length. Each is shaped like a scalpel (Text-fig. 5*a*) and ends in a straight point; the proximal part is bent slightly inwards.

Following the head proper is the cephalic peduncle (Text-figs. 4, 14, 15) measuring 0·264–0·373 mm. long, 0·052–0·088 mm. wide anteriorly, and 0·070–0·100 mm. wide posteriorly. It bears eight longitudinal rows of backwardly directed hooks, there being usually fifteen, or, occasionally, fourteen or sixteen in each row. The hooks decrease in size from before backwards and have the typical shape of the peduncle hooks of this genus, being T-shaped in surface view and having, also, a third branch or median root directed inwards (Text-fig. 7). The most anterior hooks measure 0·058 mm. in length. Passing backwards they decrease gradually to 0·014 mm. The cross-bar of the T decreases in breadth from 0·041 to 0·004 mm. and the length of the median root from 0·04 to 0·001 mm. The longitudinal rows of hooks are slightly staggered, in pairs, the two dorsal and the two ventral are opposite one another and the two lateral of one side opposite the two lateral of the other side, being slightly behind the dorsal and ventral. This is probably to accommodate the median root of each of the eight hooks. The cuticle covering the peduncle is four times as thick as that covering the head proper and the strobila (Text-figs. 14, 15). The only part of the hook to protrude from the surface is the blade which is almost straight with a very slight curve and tapers to a sharp point (Text-fig. 8). The blades are, in the resting state, directed backwards and lie close against the peduncle. The cross-bar of the T is embedded in the cuticle just outside the basement membrane (Text-figs. 14, 15). It consists of a curved bar on either side of the blade, the curve following the outline of the peduncle (Text-figs. 14, 15). Each half of the cross-bar is also slightly concave posteriorly (Text-fig. 7). The median root is directed inwards and slightly backwards at an angle of about 70° with the blade. It is a slightly curved bluntly ending bar extending well into the parenchyma in the central zone of the peduncle, those from opposite sides sometimes overlapping. These hooks, like the apical hooks, can be moved by muscles attached to them, as will be described later.

The strobila is cylindrical in unflattened specimens (Pl. 3, fig. 1; Text-figs. 21–29)



Text-figs. 9–15. *Echinobothrium brachysoma* Pintner

Text-fig. 9. Transverse section through scolex showing middle region of rostellum and musculature.

Text-fig. 10. Transverse section through scolex showing posterior region of rostellum, musculature, excretory vessels and anterior nerves.

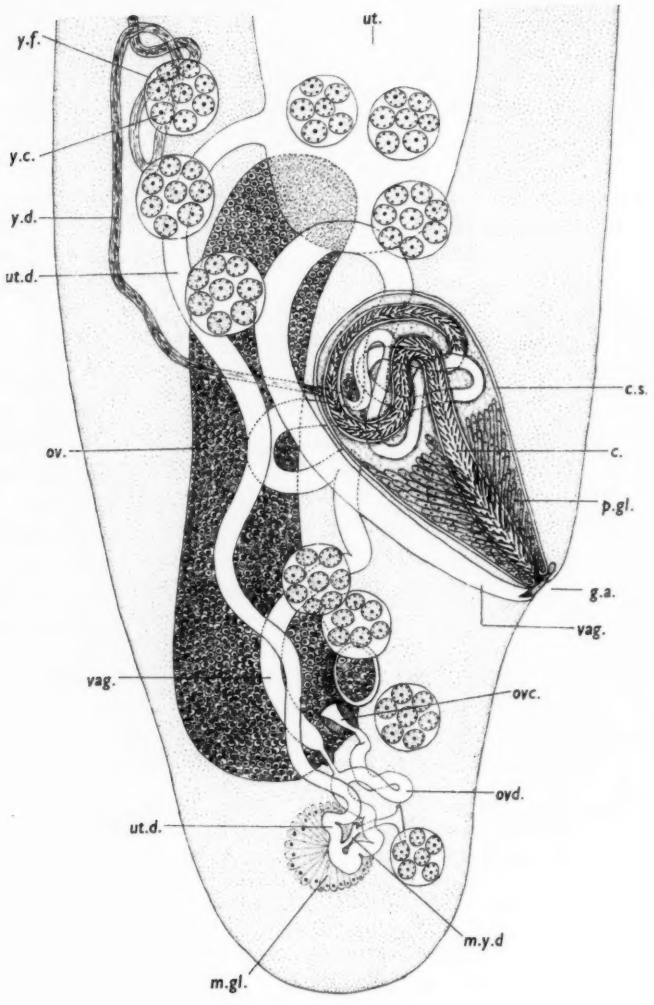
Text-fig. 11. Transverse section through scolex showing protractor muscles of rostellum and cerebral ganglia.

Text-fig. 12. Transverse section through scolex showing cerebral ganglia, median commissure and musculature.

Text-fig. 13. Transverse section through scolex showing division of each protractor into two, excretory vessels and lateral nerves.

Text-figs. 14, 15. Transverse sections through peduncle of scolex showing peduncle hooks in opposite pairs. The pairs alternate. Median hook roots embedded in skeletal material.

and measures 1·103–2·792 mm. in length. There is no neck but segmentation is indistinct immediately behind the scolex. It consists of up to 12, or rarely 14, proglottides including those incompletely formed and only the last proglottid is



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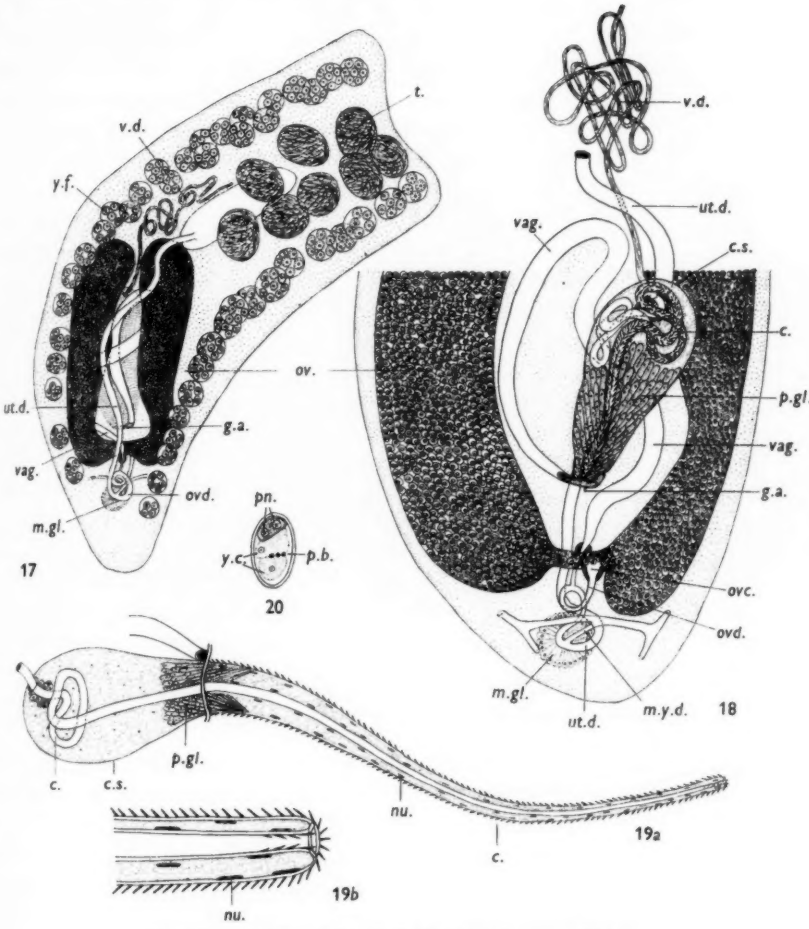
Text-fig. 16. *Echinobothrium brachysoma* Pintner. Posterior half of last proglottid, lateral view, showing genitalia.

gravid. The gravid proglottid measures 0·428–1·000 mm. long and 0·181–0·223 mm. wide. It is bead-like in shape, being distended, at first anteriorly and later along its length, by the gravid uterus. The early proglottides are broader than long, the next almost square in outline and the later ones longer than broad. A series of dimen-

sions from selected proglottides along the strobila are as follows: 0·016 × 0·064 mm.; 0·039 × 0·090 mm.; 0·126 × 0·133 mm.; 0·358 × 0·171 mm. and 0·651 × 0·204 mm. The genital atrium is on the ventral surface in the middle line near the posterior end of the proglottid (Text-figs. 16, 17, 18, 24; Pl. 3, figs. 1, 5). There is no uterine pore.

The cuticle covering the strobila is very thin, measuring 0·002 mm. or less and seems to be continuous without relation to the segmentation. In the cephalic peduncle the cuticle is 0·008 mm. in thickness.



Text-figs. 17–20. *Echinobothrium brachysoma*, Pintner

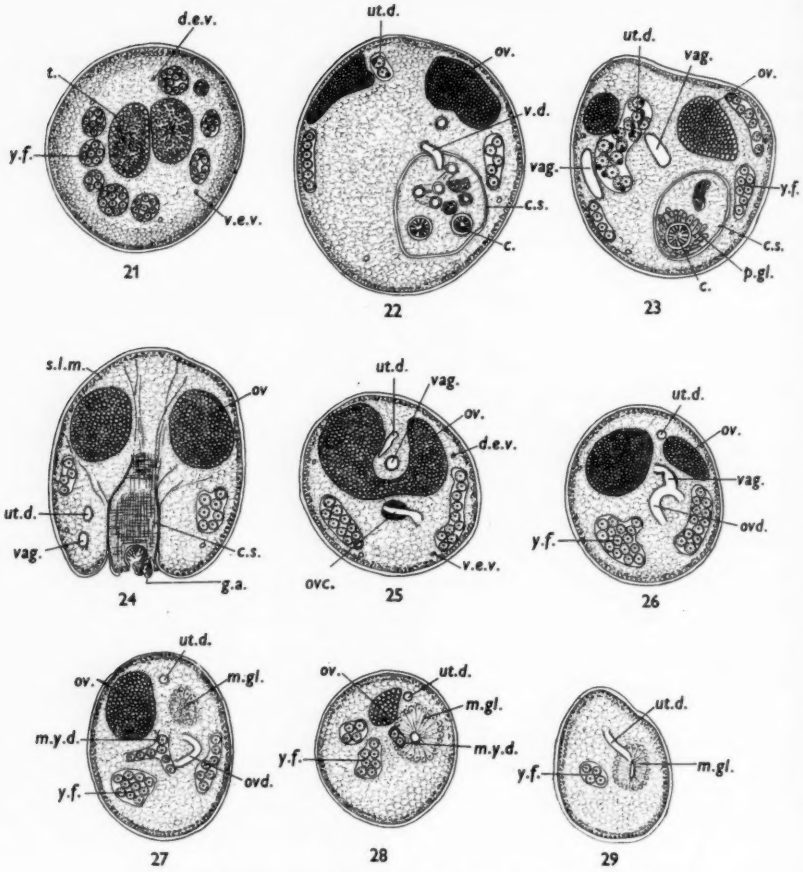
Text-fig. 17. Last proglottid, dorsal view, showing genitalia.

Text-fig. 18. Posterior end of last proglottid, ventral view, showing the arrangement of the reproductive ducts.

Text-fig. 19*a*. Cirrus-sac and evaginated cirrus.

Text-fig. 19*b*. Tip of evaginated cirrus.

Text-fig. 20. Egg.



Text-figs. 21–29. *Echinobothrium brachysoma* Pintner

Text-fig. 21. Transverse section through anterior half of proglottid showing testes and yolk follicles.

Text-fig. 22. Transverse section through proglottid showing the vas deferens entering the cirrus-sac, the ovary and uterine duct.

Text-fig. 23. Transverse section through proglottid showing cirrus-sac, ovary, uterine duct and vagina.

Text-fig. 24. Transverse section through prolgottid showing genital atrium.

Text-fig. 25. Transverse section through proglottid showing the isthmus of the ovary, the uterine duct, vagina and ovicapt.

Text-fig. 26. Transverse section through proglottid showing the vagina opening into the oviduct.

Text-fig. 27. Transverse section through proglottid showing oviduct and transverse yolk ducts joining to form the median yolk duct.

Text-fig. 28. Transverse section through proglottid showing Mehlis's gland, the median yolk duct and uterine duct.

Text-fig. 29. Transverse section through proglottid showing the uterine duct emerging from Mehlis's gland.

MUSCULATURE

The musculature of the strobila is very feebly developed. It consists of a layer of longitudinal fibres lying beneath the basement membrane (Text-figs. 21–29). In the scolex the musculature is well developed in association with the rostellum, the bothridia and the hooks.

Intrinsic muscles of the scolex

(1) *Superficial longitudinal muscles.* The superficial longitudinal muscles can be followed forwards from the early part of the strobila into the cephalic peduncle where they pass in eight bands between the eight longitudinal rows of hooks (Text-figs. 14, 15). They continue into the head proper where behind the attachment area of the bothridia they become continuous all round, being better developed laterally. Where the bothridia are attached, dorsally and ventrally, the longitudinal muscles are restricted to the lateral regions (Text-figs. 9–13). Superficial longitudinal muscles are present, also, in the bothridia themselves everywhere below the surface (Text-fig. 1). In effect, therefore, as the bothridia are not sharply demarcated from the parenchyma of the head, there is a continuous layer of longitudinal muscles everywhere in the scolex below the cuticle and basement membrane (Text-figs. 9–13). At the posterior end of the head proper these enter the bothridia and continue around the free posterior margin up the outer surface and also up the adjacent surfaces on either side. Anteriorly some of the muscles cross one another at the apex of the scolex while others are inserted into the basement membrane. Where the bothridia join the scolex posteriorly some of the longitudinal muscles fan out obliquely forwards into the bothridia as very fine fibres (Text-fig. 2). Contraction of superficial longitudinal muscles shortens the head proper, the cephalic peduncle and the bothridia.

(2) *Superficial circular muscles of the cephalic peduncle.* These occur outside the superficial longitudinal muscles in the cephalic peduncle (Text-figs. 14, 15). They tend to become arranged in circular bands between the hooks (Text-fig. 2) and their contraction will lengthen the cephalic peduncle.

(3) *Transverse muscles of the scolex and bothridia.* These are present throughout the length of the head proper. They form a band of delicate muscle fibres extending across the head dorsally and ventrally where the bothridia are attached (Text-figs. 10–13). They are first apparent near the posterior end of the rostellum and to the inner side of the protractor muscles (Text-fig. 10). As the protractors pass deeper into the centre of the scolex the transverse muscles come to lie at first on both sides of them and then mainly to the outer side (Text-figs. 11–13). They are, actually, always across the base of the bothridium dorsally and ventrally. Some are inserted into the wall of the scolex at this point while others continue out into he bothridia spreading out in them (Text-figs. 9–13) eventually being inserted into the basement membrane. Transverse muscles are also present in the free posterior portion of each bothridium. Contraction of these muscles will narrow the scolex from side to side.

(4) *Dorso-ventral muscles of the scolex and bothridia.* These, like the former, are

present throughout most of the scolex and together with them demarcate, faintly, a square area in transverse section in the centre of the scolex (Text-fig. 10). They are apparent on either side of the rostellum where the bothridia are first visible (Text-figs. 9, 10) and continue backwards to the outer sides of the excretory vessels. In the region of the cerebral ganglia they tend to spread and thereafter they are mostly to the inner side of the lateral nerves. They extend into the bothridia, dorsally and ventrally, fanning out and are inserted into the basement membrane as are the transverse muscles (Text-figs. 9–13). These muscles, like the previous, will, when they contract, narrow the diameter of the scolex and so elongate it.

(5) *Lateral diagonal muscles.* Diagonal muscles are situated laterally between the rostellum and the posterior limit of the bothridia just to the inner side of the dorso-ventral muscles on either side. They form a double series of delicate diagonal fibres which cross one another laterally and extend into the bothridia dorsally and ventrally (Text-fig. 2).

(6) *Radial muscles of the bothridia.* Delicate radial muscles are present in the lateral free parts of the bothridia throughout their length (Text-figs. 10–13).

(7) *Anterior dorso-ventral muscles.* A few dorso-ventral muscles occur at the apex of the scolex (Text-figs. 3, 4). They are inserted into the basement membrane just in front of the apical hooks. Contraction of these helps to 'close-up' the apex of the scolex when the rostellum is withdrawn and so brings the roots of the hooks close together in the middle line (Text-fig. 3).

Contractions of all these muscles bring about changes in shape and movements of the scolex and bothridia. Their contractions, however, are closely bound up with the movements of the rostellum and of the extrinsic muscles of the rostellum and the muscles of the hooks.

Rostellum

The rostellum, embedded in the anterior end of the scolex, has the shape of a laterally compressed hemisphere (Text-figs. 1, 3, 4, 9; Pl. 1, fig. 5). At rest the anterior margin lies about half way along the length of the apical hooks (Text-fig. 1). It measures 0·067–0·144 mm. in length and viewed dorsally or ventrally is rounded behind and flattened or cushion-like in front. Viewed laterally (Text-figs. 3, 4) it is broader with a maximum dorso-ventral depth, anteriorly, of 0·111 mm. In transverse section the dorso-ventral diameter can be seen to be a little more than twice the transverse diameter (Text-fig. 9). When the rostellum is protruded it has, viewed laterally, a bluntly heart shaped outline (Text-fig. 4, Pl. 2, fig. 2). The apex of the heart is posterior and the two lobes anterior, one dorsal and one ventral. The heart shape is emphasized by the anterior extremity of the scolex becoming slightly concave with the dorsal and ventral groups of hooks widely separated from one another. The rostellum is covered on all surfaces except the anterior by a transparent structureless limiting layer. The main body consists of a mass of transverse muscle fibres running from right to left and inserted into the limiting layer (Text-fig. 9; Pl. 1, fig. 5). These are uniform in arrangement throughout except for a slight change in the grouping of the fibres posteriorly. Nuclei are scattered among the fibres and at the posterior end what appears to be a tendon projects into

the rostellum as a small median bar parallel to the muscle fibres (Text-figs. 3, 4, 10). In addition to the main mass of transverse muscles other intrinsic muscles are present in the rostellum. Superficial meridional fibres lying just below the limiting layer pass upwards around the rostellum. They tend to group themselves in three zones, a central zone, the fibres of which pass up the centre of one lateral surface over the top and down the other side being continuous with the tendon posteriorly (Text-figs. 3, 4) and a dorsal and ventral zone. Some of these latter are continuous with the tendon, while others are inserted into the limiting layer posteriorly. Around the dorsal and ventral lobes are circular fibres (Text-figs. 3, 4; Pl. 1, fig. 4). Contraction of the main mass of transverse muscles of the rostellum will increase its dorso-ventral diameter. Contraction of the meridional fibres will shorten it, those of the central zone being more powerful will emphasize the heart shape. Contraction of the circular muscles around the lobes will make them a little more prominent and as they are immediately below the roots of the dorsal and ventral group of apical hooks will form a firm cushion to support them (Text-fig. 4, Pl.1, fig. 4).

Muscles of the apical hooks

The apical hooks can be moved by muscles which are attached to their roots. Their movements depend, also, on movements of the rostellum and of the scolex as a whole. The movement of the hooks consists mainly of a lifting of the blades so the muscles concerned will be referred to as hook elevator muscles.

(1) *Inner hook elevator muscles.* One of these muscles, consisting of a band of fibres, is attached to the 'handle' of each of the nine large dorsal and ventral apical hooks and to each of the small hooks on either side of them (Text-figs. 1, 6). Muscles from three hooks of the posterior row pass to one side and from the other three to the other side. Those from the median hook of the anterior row divide into two groups, one going to either side with the muscles from each outer hook. Muscles from the small hooks follow the main muscles of their own side. This arrangement can best be seen under pressure where it is accentuated but it is not induced by pressure. Behind the apices of the hooks the two main muscle bands joint to form one (Text-figs. 1, 6) which passes close around the posterior border of the rostellum (Text-figs. 3, 4, 9; Pl. 1, fig. 5), those from the dorsal and ventral sides being continuous with one another and lying immediately outside the limiting layer of the rostellum. The course of these muscles is influenced by the position of the rostellum, i.e. the degree to which it is protruded or withdrawn. When the rostellum is completely withdrawn (Text-fig. 3) the roots of the dorsal and ventral hooks are close together in the centre of the scolex. The muscles then pass back for a short distance through the centre of the scolex as far as the rostellum, where they diverge towards the dorsal and ventral sides respectively and continue around the rostellum. When the rostellum is protruded (Text-fig. 4) the roots of the dorsal and ventral hooks are far apart from one another so that the muscles then form a half hoop widely open in front and following the contour of the rostellum.

(2) *Outer hook elevator muscles.* There is again a dorsal and a ventral group of these muscles associated, respectively, with the dorsal and ventral hooks. They, also, are inserted into the 'handles' of both the large and small apical hooks, the in-

sertions overlapping, to some extent, those of the inner hook elevator muscles (Text-fig. 5*c*). From the hooks they pass backwards and outwards in a fan-like manner, being almost equal in length to the hooks themselves. They are inserted into a limiting layer which is continuous anteriorly with the basement membrane of the body wall (Text-fig. 4). In the resting state they lie in front of the rostellum (Text-fig. 3) occupying the space to the dorsal and ventral sides, respectively, of the inner hook elevator muscles. When the rostellum is protruded and the hooks raised the muscles become more conspicuous as the body wall is expanded behind the hooks into a well-defined dorsal and ventral lobe (Text-fig. 4) in which the muscles spread out. In the resting state this lobe becomes a fold lying just underneath the apices of the hooks (Text-figs. 2, 3). The limiting layer continues around the rostellum outside the inner hook elevator muscles.

Extrinsic muscles of the rostellum and hook apparatus

The movements of the rostellum and hooks are, to a certain extent, dependent on one another, the same extrinsic muscles being concerned in the movements of both.

(1) *Protractor muscles of rostellum.* Powerful dorsal and central protractor muscles pass forwards through the head proper, diverging one to the dorsal and one to the ventral side of the rostellum (Text-figs. 3, 4). Each muscle measures 0·011-0·017 mm. in diameter and consists of a bundle of about thirty-six fibres (Text-figs. 10–12). Anteriorly each muscle narrows to become continuous with a tendon 0·003 mm. in diameter (Text-figs. 1, 3, 4, 9; Pl. 2, fig. 5). The tendon passes up the mid-dorsal or mid-ventral side of the rostellum and is inserted into the limiting layer covering the outer hook elevator muscles where this is continuous with the basement membrane of the body wall (Text-fig. 4). Posteriorly, near the limit of the head proper the muscle splits into two bundles which diverge from one another and are inserted dorso-laterally and ventro-laterally on either side into the basement membrane of the body wall where the head proper joins the cephalic peduncle (Text-figs. 1, 13; Pl. 2, fig. 5). Contraction of these powerful muscles plays an important part in the movements of the rostellum and consequently of the hooks, as will be described later.

(2) *Anterior circular muscle band.* Closely associated with the roots of the hooks and immediately to the inner side of them is a well-developed band of circular muscle fibres seen best when the rostellum is withdrawn (Text-figs. 1, 2, 6). They are not attached to the hooks but enclose the anterior portions of the inner and outer hook elevator muscles. When the rostellum is protruded they are so stretched that they are hardly visible. They are concerned with the movements of the hooks.

Elevator muscles of peduncle hooks

The hooks of the peduncle also have muscles attached to them which are, as in the case of the apical hooks, elevator muscles. Attached to each median portion of the hook root is a number of muscle fibres (Text-fig. 8). These pass backwards and outwards to be inserted into the basement membrane in a fan-like manner

immediately in front of the next hook in the longitudinal row. Contraction of these muscles would pull the roots downwards and consequently raise the blades. The peduncle hooks are steadied in their movements by what appear to be strands of a skeletal material which pass down the basement membrane around the median root towards the centre of the peduncle. This portion of the root is, in fact, embedded in this material (Text-figs. 14, 15) which is continuous, across the centre of the peduncle, with that surrounding the opposite hook root. Two dorsal and two ventral hook roots are connected in this way (Text-fig. 14) and two lateral from either side (Text-fig. 15) forming a series of X-shaped groups of fibres alternating along the length of the peduncle. This is another reason why the hooks of the peduncle are slightly staggered in arrangement.

Movements of scolex, rostellum and hooks

General movements of the scolex and bothridia are brought about by the general musculature of the scolex both superficial and deep. The scolex can be lengthened or shortened and the bothridia themselves achieve, presumably, quite a high degree of mobility along their free margins. These movements of the scolex can be quite independent of the movements of the rostellum and hooks as the scolex can be expanded and contracted while the hooks are at rest and the rostellum remains withdrawn. The converse, however, is not the case as movements of the rostellum and hooks involve some of the muscles of the scolex.

Movements of the rostellum and apical hooks will alter quite considerably the general outline of the scolex (Text-figs. 2–4). The shape of the rostellum is controlled partly by its intrinsic muscles, partly by its protractor muscles and partly by the elevator muscles of the apical hooks which are closely associated with it. In order that the scolex may anchor itself in the tubular crypts in the intestinal wall of the host the dorsal and ventral groups of apical hooks must be raised (Text-fig. 4; Pl. 2, fig. 2) and the region of the head where they occur must be elongated in the dorso-ventral plane so that the hooks may come in contact with the surface to which they will adhere (Pl. 1, fig. 4). The hook roots also must rest on a firm foundation so that they can pierce the mucosa; the rostellum forms a cushion-like support for this latter purpose.

Contraction of the intrinsic transverse muscles of the rostellum will elongate it and consequently the scolex in a dorso-ventral direction (Pl. 1, figs. 4, 5). Contraction of the intrinsic longitudinal muscles will assist in this by shortening the rostellum in the antero-posterior direction. As the muscles in the central zone appear to be the most powerful a concavity will be formed on the anterior face of the rostellum (Text-fig. 4; Pl. 1, figs. 3, 4; Pl. 2, fig. 2). This results in the pushing up of a cushion-like lobe dorsally and ventrally below the roots of the apical hooks. Contraction of the circular muscles around these two lobes will emphasize this and will strengthen the support for the hooks (Pl. 1, fig. 4). The protrusion of the rostellum depends on the protractor muscles and on the inner hook elevator muscles. As already indicated the tendons of the two protractor muscles are inserted mid-dorsally and mid-ventrally into the limiting layer which encloses the rostellum and

the hook elevator muscles (Text-figs. 3, 4; Pl. 2, fig. 5). Contraction of the two protractors will pull back the limiting layer mid-dorsally and mid-ventrally lengthening the anterior margin of the scolex in the dorso-ventral plane. The dorso-ventral muscles here relax so that the dorsal and ventral groups of apical hooks separate from one another and the rostellum is pushed up between them (Text-fig. 4; Pl. 2, fig. 2). At the same time the inner hook elevator muscles contract, raising the hooks and as they pass around the rostellum posteriorly, from the dorsal to the ventral side, they help the protractor muscles to push the rostellum forwards. The contraction of the outer hook elevator muscles will also assist in raising the hooks and in broadening the scolex.

Relaxation of the intrinsic muscles of the rostellum, the protractors and the elevator muscles of the hooks allows the structures concerned to return to a resting state (Text-figs. 2, 3). Contraction of the anterior dorso-ventral muscles help to 'close up' the scolex anteriorly, bringing the roots of the dorsal and ventral groups of hooks close together. The anterior circular muscle band which surrounds the inner and outer hook elevator muscles will, on contraction, compress these muscles and help still further to bring the roots of these hooks together with the blades directed backwards.

As already indicated the penduncle hooks are elevated by the contraction of the elevator muscles passing from the median root, in each case, to the basement membrane close behind (Text-fig. 8). The hooks return to their resting state when these muscles relax aided, probably, by the elasticity of the skeletal material in which the median root of the hook is embedded.

Attachment of the worm to the intestine of the host and the effect on the host tissues

To understand the mode of attachment of the scolex to the wall of the spiral valve of the host, *Raja clavata*, the structure of the wall must first be described. Viewed from the internal surface the spiral valve has a honeycombed appearance, being covered with numerous pores of slightly varying size and outline (Pl. 1, fig. 1). These are actually the openings of tubular crypts placed close together all over the surface and opening into the lumen. In infested fishes the worms have their scolices buried in the crypts, the posterior part of the strobila hanging free in the lumen of the spiral valve (Pl. 1, fig. 2). Horizontal and vertical sections through the wall show the tubular crypts clearly (Pl. 1, figs. 3–6; Pl. 2, fig. 3). The spiral valve, including the crypts, is lined by a continuous layer of columnar epithelial cells which have a striated border and a basal nucleus (Pl. 1, figs. 3–6; Pl. 2, figs. 3–5). Numerous goblet cells filled with mucus and opening into the lumen are scattered among the columnar cells. Other goblet cells contain granules, presumably zymogen granules (Pl. 1, fig. 6). The crypts rest on a stratum compactum, consisting of fibres and scattered cells, which extends up around the epithelium lining the crypts (Pl. 1, fig. 3; Pl. 2, figs. 3–5). The depth of the crypts is fairly uniform, being about 0·805–0·948 mm., they are circular, oval or slightly irregular in transverse section and the epithelial layer measures 0·020–0·029 mm.

in depth. Measurements taken from three selected crypts, in transverse section, are as follows: diameter including epithelial layer (1) 0·176 × 0·088 mm. (lumen 0·117 × 0·008 mm.), (2) 0·270 × 0·100 mm. (lumen 0·190 × 0·008 mm.), (3) 0·185 × 0·091 mm. (lumen 1·132 × 0·008 mm.).

Echinobothrium brachysoma is admirably suited to adhere to a surface of this kind. Indeed, it is unlikely that it could adhere to any other kind of surface. As previously mentioned each worm lies with the scolex buried in a crypt, the depth of the crypt being a little greater than the length of the scolex (Pl. 2, fig. 3). To enter the crypt with the least amount of resistance the scolex would need to be as narrow as possible. Narrowing is achieved by contraction of the transverse and dorso-ventral muscles of the head proper and of the circular muscles of the cephalic peduncle. The scolex thus elongates to its maximum and the apical hooks lie close against the head, their roots almost touching in the centre. They are maintained in this position by the contraction of the anterior band of circular muscles and the anterior dorso-ventral muscles. The apex of the scolex thus forms a rigid probe which can be thrust into the opening of the crypt. The peduncle hooks also lie close against the peduncle. All the hooks will be pointing backwards and the tips which curve slightly inwards will not come in contact with the wall of the crypt. The slightly curved outer surfaces of the hooks will slide against the epithelium without causing damage (Pl. 2, fig. 1). When well inside the crypt the apical hooks must be raised and must penetrate the epithelial lining to anchor the worm firmly. The longitudinal muscles of the head proper now contract, increasing its diameter so that it comes nearer to the crypt wall. This contraction may account for the fact that the tip of the scolex is almost always a little distance from the apex of the crypt (Pl. 2, figs. 1–3). The apical hooks are then raised and the rostellum protruded in the manner already described. The hooks will then be pushed against the wall of the crypt and will eventually puncture it (Pl. 2, fig. 2). Further contraction of the scolex or early part of the strobila will result in the hooks becoming more deeply embedded. The small apical hooks are usually at this time directed straight forwards (Text-fig. 4) and penetrate the epithelium, directly in front of the scolex, where the lumen has not been dilated (Pl. 2, fig. 2). Crypts containing worms will, of course, become somewhat distended and more circular in outline when seen in transverse section (Pl. 1, figs. 3–6).

The peduncle hooks can be raised by the contraction of their elevator muscles and may penetrate the wall of the crypt, but this seems to be somewhat unusual. It is extremely doubtful whether the worm could move from one crypt to another unless the mucosa was so damaged that it was torn away completely. It is impossible to detach a specimen, after fixation, without damaging the intestine as the crypt comes away with it like the finger of a glove, the hooks still firmly embedded (Pl. 2, fig. 2). With care the crypt wall can be teased away leaving the worm with the hooks raised and the rostellum protruded (Text-fig. 4).

The presence of the worm will naturally have some adverse effect on the mucosa of the host. The crypt is stretched and follows the outline of the scolex and bothridia (Pl. 1, figs. 3–6). There is a flattening of the epithelial cells where the pressure is greatest. The tips of the hooks tear the epithelium where they penerate

(Pl. 1, figs. 3, 4). They may even extend into the stratum compactum. The damage is usually localized to the area around the hooks and no particular response has been noticed on the part of the host tissues. Only in a few cases have the peduncle hooks been observed to penetrate the wall of the crypt. Sudden fixation, *in situ*, in such cases may cause the muscles of the scolex to contract violently so that a strip from the surface of the epithelium is torn off over a large area (Pl. 2, fig. 4).

Nervous system

It is impossible to make out more than the essential arrangement of the central elements of the nervous system.

There is a cerebral ganglion, consisting of a dorsal and ventral lobe, on either side a short distance behind the rostellum (Text-figs. 1, 4, 11). They are connected with one another across the centre of the scolex by a median commissure (Text-figs. 1, 12). Arising anteriorly from the extremity of each lobe of both ganglia is an anterior nerve (Text-figs. 1, 4, 10). These pass forwards two on either side of the rostellum. As the rostellum widens to its maximum the anterior nerves lie close to the limiting layer and can be followed forwards for a short distance. They become smaller in diameter and are eventually lost to view. Presumably they innervate the rostellum and elevator muscles of the hooks. Arising posteriorly from each ganglion is a lateral nerve (Text-figs. 1, 4) which passes backwards on either side through the scolex (Text-figs. 13–15) and into the strobila.

Excretory system

Four longitudinal excretory vessels extend throughout the strobila, two dorsal and two ventral on either side (Text-figs. 21–25). In the scolex they pass up into the cephalic peduncle (Text-figs. 14, 15; Pl. 2, fig. 4) weaving their way between the median roots of the peduncle hooks, enter the head proper and continue up the centre (Text-figs. 1, 4, 13). Opposite the point where the bothridia become free from the scolex, posteriorly, the right and left vessels, dorsally and ventrally respectively, are united by a transverse vessel (Text-fig. 1). The two transverse vessels lie parallel to one another in the centre of the scolex to the inner side of the protractor muscles of the rostellum and behind the median nerve commissure. The two dorsal and two ventral vessels then turn outwards (Text-fig. 12) passing to the outer side of the protractor muscles and into the bothridia (Text-figs. 4, 11, 12). They take a forward, slightly undulating course and just beyond the posterior limit of the rostellum the dorsal joins the ventral vessel of its own side forming a slightly undulating loop (Text-fig. 4; Pl. 4, fig. 5).

Genitalia

There is one set of reproductive organs in each proglottid. The genital atrium is a transversely oval aperture $0{\cdot}038 \times 0{\cdot}008$ mm. situated on the ventral surface in the middle line near the posterior end of the proglottid (Text-figs. 16–18; Pl. 3, figs. 1, 5). Into the genital atrium open the cirrus and slightly to the right and a little behind it, the vagina. There is no uterine pore. There is only one gravid proglottid easily distinguished in the complete worm attached to the intestine of the

host (Pl. 1, fig. 2), the eggs in the uterus appearing as a dark patch through the body wall (Pl. 3, figs. 1, 5). Anlagen of the testes are present early. They develop gradually and persist to the last proglottid. The female organs develop more slowly and are only fully formed in the last proglottid.

(1) *Male reproductive system.* The number of testes quoted for the species is 6–8. I find the number may be 6–9 and it is not always constant in every proglottid in the same strobila. Counts made in six successive proglottids in four different worms were as follows: 6, 6, 6, 6, 7, 6; 6, 6, 7, 7, 8, 7; 7, 6, 9, 8, 8, 9; 7, 8, 9, 9, 9, 8. The testes appear early in the strobila as darkly staining bodies, even before segmentation is complete. They are at first closely packed together so that they become wedge-shaped. Passing backwards and as the proglottides increase in size the testes separate from one another and become spherical or oval in shape, measuring 0·168 × 0·115 mm. to 0·194 × 0·090 mm. They are arranged in two rows in the central region of the anterior half of the proglottid (Text-figs. 17, 21). The vas deferens is very long and coiled, lying in the mid-dorsal line just in front of the ovary (Text-figs. 16–18). It measures 0·005–0·010 mm. in diameter, is packed with sperms and probably functions as a vesicula seminalis. It enters the cirrus-sac subterminally on the dorsal side (Text-figs. 16–18, 22). The cirrus-sac is pyriform in shape, measuring 0·117 × 0·073 mm. to 0·132 × 0·067 mm. It is directed postero-ventrally (Text-fig. 16), the narrow end protruding slightly into the genital atrium. The wall of the cirrus-sac is provided with circular and longitudinal muscles (Text-fig. 24), the contraction of which forces the cirrus to evaginate. On entering the cirrus-sac the vas deferens is thrown into coils in the proximal third of the sac. It measures about the same or a little more in diameter than it does outside the cirrus-sac. It becomes continuous, eventually, with the cirrus which in the resting state is invaginated (Text-figs. 16, 18, 22, 23). The proximal part of the invaginated cirrus runs straight up the centre of the cirrus-sac (Text-figs. 16, 18) for about three-quarters of its length and is then thrown into one or two loops before becoming continuous with the vas deferens. The widest proximal part measures 0·017 mm. in internal diameter and the narrow distal part, which will be the apex when evaginated, measures 0·008 mm. The cirrus was not found evaginated in any of the specimens but was induced to evaginate by pressure on the coverslip in a mounted living worm (Pl. 3, fig. 5). The evaginated cirrus measures 0·470 mm. in length and tapers from 0·044 mm. in diameter at the base to 0·008 mm. at the apex (Text-fig. 19*a*, *b*). The cuticle is covered with fine backwardly directed spines measuring 0·0039 mm. in length (Text-fig. 19*a*, *b*) which are also clearly visible in the invaginated state (Text-figs. 16, 18, 22, 23). A layer of cytoplasm containing elongated nuclei covers the invaginated cirrus and a part of the vas deferens (Text-fig. 16). This layer is visible, also, in the evaginated cirrus filling the space between the outer and inner walls (Text-fig. 19*a*, *b*). Within the cirrus-sac, occupying the distal half, is a number of unicellular, possibly prostate, gland cells (Text-figs. 16, 18, 19*a*, *b*, 23). They surround the proximal part of the invaginated cirrus and appear to open into it. There is also a group of rounded cells surrounding the vas deferens immediately after it enters the cirrus-sac (Text-figs. 16, 19*a*, *b*). The remainder of the cirrus-sac is filled with highly vacuolated parenchyma.

(2) *Female reproductive system.* The ovary is situated at the posterior end of the proglottid and lies dorsal to the cirrus-sac (Text-figs. 16–18, 22–26). It is bilobed, the two elongated lobes being joined by an isthmus near the posterior end. Each lobe measures 0·170 × 0·191 mm. in length, 0·038–0·041 mm. in breadth and 0·044–0·073 mm. in depth. The isthmus measures 0·020 mm. in length and 0·014 mm. in diameter and the ova 0·004 mm. The oviduct arises as a well-developed thick walled ovicapt, 0·017 mm. in diameter, from the posterior side of the isthmus just where the latter joins the left lobe of the ovary (Text-figs. 16–18, 25); occasionally it arises nearer the right lobe. The oviduct, 0·003 mm. in diameter, continues posteriorly soon forming a loop which turns forwards and towards the middle line where it receives the vagina (Text-figs. 16–18, 26). From its opening into the genital atrium the vagina passes forwards dorsal to the cirrus-sac between the lobes of the ovary. Just in front of the cirrus-sac it turns backwards and to one side forming, almost, a loop around the cirrus-sac (Text-figs. 16–18, 23). The diameter along this part of its length is uniform and measures 0·008–0·011 mm. Near the isthmus the vagina narrows suddenly to form a duct 0·002 mm. in diameter which passes dorsally to the isthmus to open into the oviduct. At the point where the vagina narrows the wall is much thickened (Text-fig. 16). Having received the vagina the oviduct continues posteriorly, in a slightly undulating course for a short distance, then receives the median yolk duct on its ventral side (Text-figs. 16–18, 27, 28). This region is surrounded by Mehlis's gland which measures 0·044 mm. in diameter. The oviduct emerges from Mehlis's gland as the uterine duct 0·004–0·020 mm. in diameter which passes forwards dorsally to the vagina and isthmus, between the lobes of the ovary in a slightly sinuous course and eventually opens into the uterus on its dorsal surface just in front of the cirrus-sac (Text-figs. 16, 17, 22–29). There are four or five rows, each of fifteen to twenty yolk follicles, extending along the length of each side of the proglottid (Text-fig. 17). In transverse section they are seen to follow the contour of the body on either side (Text-fig. 21) in the anterior region. Posteriorly, in the region of the ovary, they may be reduced in number. The longitudinal yolk ducts could be traced at the posterior end where, level with the posterior end of the ovary, a transverse yolk duct arises on either side. These meet in the centre, ventrally, to form a median yolk duct which opens into the oviduct. The yolk cells resemble those of the Digenea. There is a central nucleus and a layer of yellow shell globules around the periphery.

The uterus is a simple oval sac. At first it lies in front of the cirrus-sac ventral to the testes and measures 0·324 × 0·207 mm. As eggs pass into it it expands to fill, first, the anterior half of the proglottid and later it extends posteriorly dorsal to the ovary filling the proglottid. No diverticula are given off from it (Text-fig. 17).

Each oocyte on entering the uterine duct has acquired two yolk cells which become arranged in tandem behind it (Text-fig. 23). By the time they reach the uterus the eggs are oval, measuring 0·022 × 0·015 mm., and are surrounded by a yellowish-brown capsule. There is no sign of an operculum or of any appendages. The eggs, however, may adhere together in groups of two to a few (Pl. 3, fig. 5). They resemble the eggs of the Pseudophyllidea or possibly the Trypanorhyncha

rather than those of the Tetraphyllidea, Proteocephaloidea or Taenioidea. The yolk cells resemble those of the Digenea in structure but as in the Taenioidea are very few in number. Sections of some eggs have been obtained in the parent uterus (Text-fig. 20). The contained structures have been interpreted as the male and female pronuclei, polar bodies and the two yolk cells. The latter are now devoid of the yellow shell globules which have presumably formed the capsule.

DISCUSSION

The original description of *Echinobothrium brachysoma* Pintner (1889) was brief, but there is sufficient information to compare it with the present specimens. A comparison is given in Table 1 which includes, also, details of *E. typus* van Beneden from the descriptions by van Beneden (1849, 1861) and Pintner (1889).

Table 1. *A comparison of* Echinobothrium brachysoma, *Pintner with the present specimens and with* E. typus *van Ben.*

	E. brachysoma Pintner (1889)	Present specimens	*E. typus* van Ben. (1849, 1861)	*E. typus* Pintner (1889)
Length of worm	1·6 mm.	1·66–2·713 mm.	5·0–6·0 mm.	6·0 mm.
Length of scolex	0·250 mm.	0·197–0·253 mm. (head proper) 0·532–0·597 mm. (incl. peduncle)		0·65 mm. (including peduncle)
No. of large hooks in each apical group	9	9	7, 9–16	? 7
Length of large hook	*c.* 0·052 mm.	0·064–0·073 mm.	—	0·044–0·046 mm.
No. of spines in row on peduncle	14	14–16	12–13	—
Size of these spines (length × breadth)	—	0·044 × 0·041 mm. (across 'wings')	—	0·05 × 0·032 mm. (across 'wings')
No. of proglottides	6 clear	*c.* 6 clear, up to 12 including early ones	8–10	14 clear
No. of testes	6–8	6–9	—	8–10
Eggs	—	0·022 × 0·015 mm.	0·01 mm.	0·01 mm.
Host	*Raja batis* L.	*R. clavata* L.	*R. clavata* L.	—

From this it can be seen that the present specimens resemble *E. brachysoma* more closely than they do *E. typus*. The former is very much smaller than the latter. Pintner described *E. brachysoma* as small and stout with the last proglottid completely ripe because the uterus is full of eggs and fills the whole inner part. That is the case here. Pintner gave the length of the scolex of *E. brachysoma* as 0·250 mm., but did not indicate whether this measurement included the cephalic peduncle. In the present specimens the head proper measures 0·197–0·259 mm., which agrees with Pintner's measurement, but the entire scolex measures 0·532–0·597 mm. which is still a little less than that given for *E. typus*. Joyeux & Baer (1936) gave a much smaller measurement for the scolex of *E. typus*, stating that the head

measures 0·12 mm. and the scolex 0·36 mm. The scolex is, however, very contractile and can vary very much according to its state at the time of fixation. The number of large apical hooks in each group seems to be debatable in *E. typus*, but seven seems to have been accepted by later workers. They are smaller than in *E. brachysoma*. There are more peduncle hooks in each of the eight rows in *E. brachysoma* than in *E. typus* and according to my measurements they are shorter but broader across the 'wings'. As already indicated the number of testes in my specimens is variable in different proglottides in the same worm so it is not a very reliable diagnostic feature. Pintner gave no measurement for the eggs of *E. brachysoma* but I find they are twice the size of those of *E. typus*. The host is different but that may not be significant provided the internal surface of the spiral valve is suitable.

Echinobothrium affine Diesing

Echinobothrium affine Diesing (1863) was first recorded from the spiral valve of *Raja clavata* L., *R. aspera* Flem. (=*R. fullonica* L.) and *R. radula* Thompson (=*R. circularis* Couch). The present specimens, given to me by Dr H. H. Williams, were obtained from *R. clavata* from the Butt of Lewes in September 1957 and from the same host species at Plymouth in August 1957 and August 1958. All the specimens were fixed after removal from the host and whole mounts and sections have been prepared as in the previous species.

Diesing (1863) in separating *E. affine* from *E. typus* mentioned that, among other features, the last proglottid is five times longer than broad and that the eggs have each a single flagellum. Both these features are clearly apparent (Pl. 3, figs. 2, 6). Pintner (1889) in his revision of the genus included *E. affine* as one of the then known four species of the genus. He stated that it had two groups of eleven large apical hooks, more than twenty hooks in each longitudinal row on the peduncle, no neck, a cirrus-sac in the middle of the proglottid, a vagina without an ascending branch and eggs, with a flagellum, lying in longitudinal strings up to 3 mm. long within a covering. Pintner gave a brief description of the complete worm and described and drew a series of transverse and longitudinal sections through the scolex which show the musculature and nervous system. He did not reconstruct these and made little mention of the function and movements of the various parts, nor did he deal with the mode of attachment of the worm to the spiral valve of the host. Southwell (1925) included Pintner's key for the four species but did not describe *E. affine*. Joyeux & Baer (1936) recorded it from *R. clavata* L., *R. fullonica* L. and *R. oxyrhynchus* L. at Nice and gave a few diagnostic features.

The scolex of *E. affine* resembles, in essential features, that of *E. brachysoma* and presumably functions in the same way. It will not be described fully here but will be compared briefly with that of *E. brachysoma*. The genitalia are described in detail.

SCOLEX, EXTERNAL FEATURES AND MUSCULATURE

Echinobothrium affine is much longer than the previous species, measuring with its one gravid proglottid (Pl. 3, fig. 2) 5·00–6·883 mm. in length with a maximum breadth, in the gravid proglottid, of 0·363–0·509 mm. The scolex measures up to

0·850 mm. in length and consists of a head proper 0·312 mm. long and a cephalic peduncle 0·538 mm. There is a dorsal and a ventral bothridium covered on all surfaces with small spines, a muscular apical rostellum and a dorsal and ventral group of eleven large hooks (Pl. 4, figs. 1–3) flanked on either side by three small hooks. As in *E. brachysoma* the large hooks are arranged in two rows, there being five in the anterior row and six in the posterior row. The central hook is the longest and the sequence and arrangement of the others is very similar to that in *E. brachysoma*. The hooks are provided with the same two series of elevator muscles which can be seen in optical section in a scolex viewed laterally (Pl. 4, fig. 1). The inner hook elevator muscles pass down the centre of the scolex and then diverge around the rostellum, being continuous behind it. The outer hook elevator muscles are arranged in the same fan-like manner as in the former species and are inserted into a limiting layer which is continuous, anteriorly, with the basement membrane of the body wall and which encloses, posteriorly, the rostellum and the inner hook elevator muscles. The two protractors of the rostellum are present and also the anterior circular muscle band (Pl. 4, fig. 2). This band of muscles, as in *E. brachysoma*, surrounds the hook elevator muscles just behind the point where they are attached to the hooks. The remaining musculature of the scolex is as in *E. brachysoma*. Superficial longitudinal muscles are present everywhere below the body wall. Transverse dorso-ventral muscles of the scolex are present in the same positions and the diagonal muscles, seen in lateral view (Pl. 4, fig. 2), are well developed. As the structure of the scolex is almost identical with that of *E. brachysoma* it seems legitimate to assume that it functions in the same way. The species occurs in the spiral valve of the same host species and is equally well adapted to adhere to a surface of this kind.

The cephalic peduncle measures 0·092 mm. in diameter anteriorly and broadens slightly to 0·115 mm. posteriorly. There are 26–28 hooks in each of the eight longitudinal rows. They are similar in shape to those of *E. brachysoma* and decrease in size posteriorly. The same elevator muscles are present.

Strobila

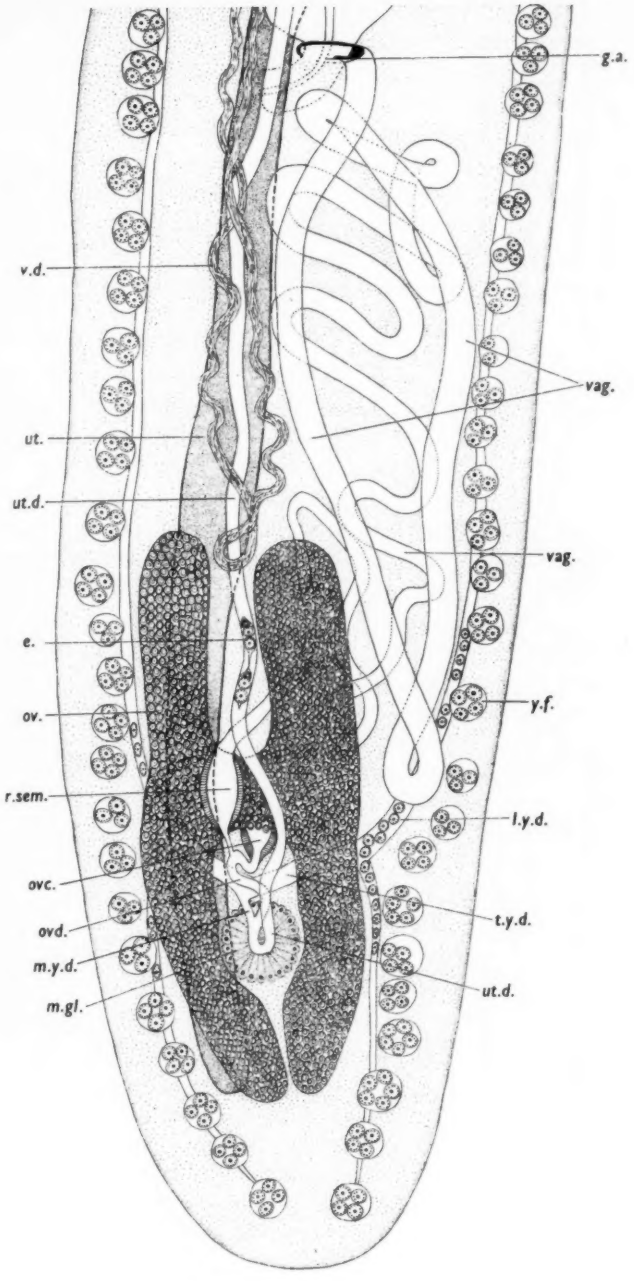
The strobila is cylindrical and measures 4·150–6·033 mm. in length. There is no neck. There are eight clearly defined proglottides which are at first slightly broader than long, but not as much so as in *E. brachysoma*, then longer than broad (Pl. 4, fig. 4) until the last proglottid measures about half the total length of the worm (Pl. 3, fig. 2). Measurements of selected numbered proglottides along the same strobila are as follows: (1) 0·114 × 0·132 mm.; (6) 0·586 × 0·223 mm.; (7) 1·524 × 0·311 mm. and (8) 2·691 × 0·456 mm. The cuticle covering the strobila is thin and again continuous without relation to the segmentation. The anlagen of the reproductive organs appear in the first proglottid as a darkly staining mass and in the third the testes and ovary can be seen as two separate areas. Individual testes are distinguishable in the fourth proglottid. The female organs develop more slowly and are fully functional, probably, only in the seventh proglottid. The last proglottid is gravid, the uterus extending, eventually, along its whole length (Pl. 3, figs. 2, 6) being packed with eggs which are arranged end to end in long bead-like

strings. The genital atrium, a transversely oval aperture measuring 0·058 mm. in width, is mid ventral and just in front of the middle of the length of the proglottid (Pl. 3, fig. 3). The cirrus opens a little in front of and to one side of the vagina. The vagina and cirrus-sac approach the genital atrium from opposite directions and are not side by side as in *E. brachysoma* where the genital atrium is posterior. There is no uterine pore.

Genitalia

(1) *Male reproductive system.* The number of testes given for this species is 8–10. I have found 8–14. They may again be variable from one proglottid to another in the same worm. Counts from four individual worms for proglottides 4–7 inclusive were as follows: 11, 14, 14, 12; 11, 13, 12, 12; 9, 8, 10, 12; 12, 13, 11, 9. Where first apparent as separate structures, in proglottid 4, the testes are closely packed and wedge shaped, being broader on the outer side and narrower towards the centre. They measure 0·034 mm. in transverse diameter and 0·011 mm. in length on their outer margins. As the proglottides elongate the testes become rounded or oval and separate from one another (Pl. 4, fig. 4). They measure, finally, 0·067 × 0·038 mm. to 0·076 × 0·056 mm. and are arranged in a double row in the anterior half of the proglottid in front of the cirrus-sac and between the yolk glands of either side. The vas deferens is not as long as in *E. brachysoma*. It extends backwards dorsally to the cirrus-sac as far as the anterior end of the ovary (Text-figs. 30, 32) where it loops round to form an ascending branch which passes forwards and eventually opens into the anterior end of the cirrus-sac (Text-fig. 31; Pl. 3, figs. 3, 4). The vas deferens measures 0·011–0·017 mm. in diameter. It is packed with sperms and for a short distance before it enters the cirrus-sac is surrounded by cells which are probably glandular. In *E. brachysoma* similar cells are present around the vas deferens immediately after it has entered the cirrus-sac. The cirrus-sac is oval, measuring 0·235 × 0·147 mm. to 0·191 + 0·155 mm. It is directed posteroventrally towards the genital atrium. On entering the cirrus-sac the vas deferens is thrown into coils (Pl. 3, figs. 3, 4) which are not, as in the previous species, confined to the proximal third of the sac but extend more than half way along its length. Inside the cirrus-sac the vas deferens narrows in diameter to 0·004–0·008 mm. It eventually becomes continuous with the cirrus which gradually increases to a diameter of 0·010–0·026 mm. and which in the invaginated state is coiled inside the cirrus-sac. The coils are more extensive than in *E. brachysoma* as the cirrus is longer and the arrangement is less constant. Unicellular glands, probably prostate, are again present around the proximal part of the cirrus but are smaller and fewer in number than in the previous species. The evaginated cirrus is very long, measuring 2·064 mm. (Pl. 3, fig. 2). It is 0·058 mm. in diameter at the base and tapers to 0·010 mm. at the apex. The wall is 0·010–0·026 mm. thick and covered with backwardly directed spines throughout its length. The same elongated nuclei are present below the wall as in the previous species. Specimens are frequently found with the cirrus in the gravid proglottid evaginated which is rarely the case in *E. brachysoma*. It is possible that this very long cirrus, once it has been evaginated, cannot be withdrawn.

(2) *Female reproductive system.* The ovary is bilobed and lies in the posterior part



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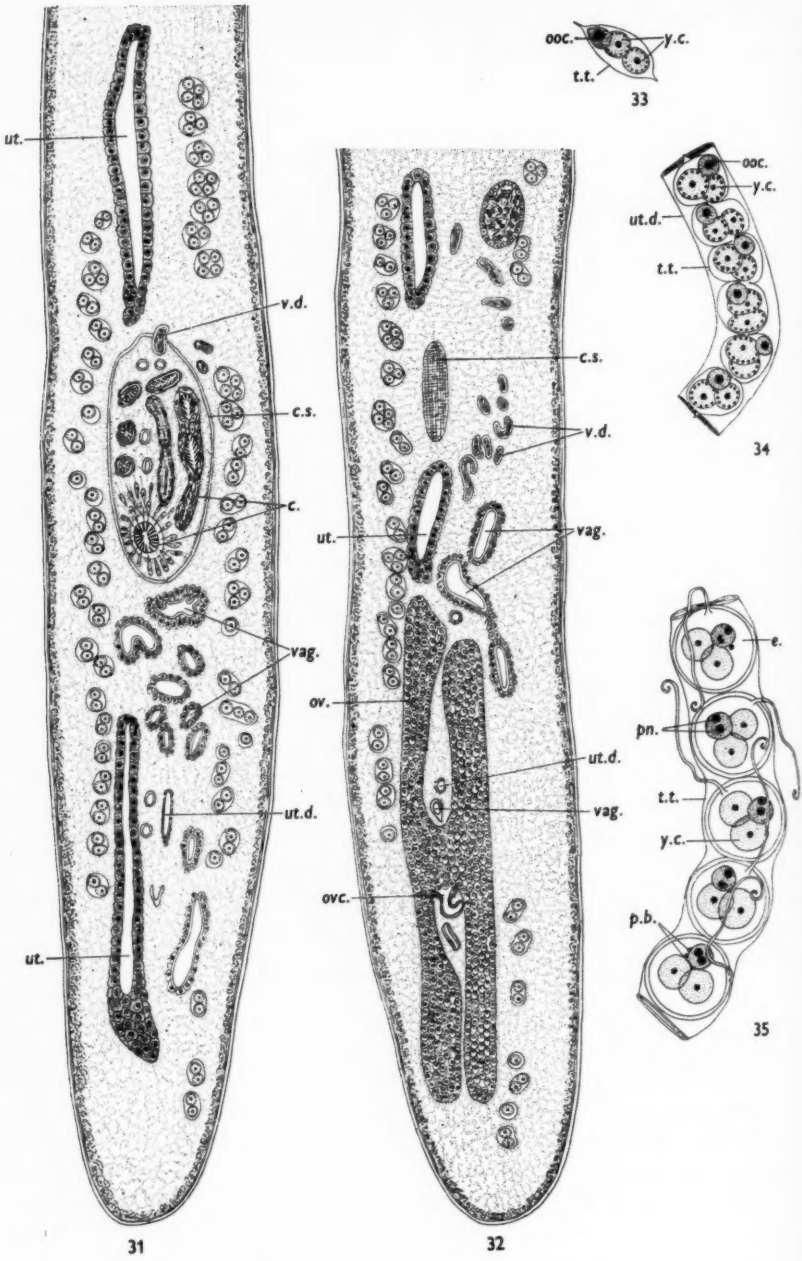
Text-fig. 30. *Echinobothrium affine*, Diesing. Posterior half of mature proglottid, dorsal view, showing genitalia.



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of the proglottid behind the cirrus-sac (Text-figs. 30, 32, 37–39; Pl. 3, fig. 3). The two lobes are united by an isthmus, at about the middle of their lengths, which is further forwards than is the case in *E. brachysoma*. Each lobe measures 0·507–0·584 mm. in length, 0·058 mm. in depth and 0·507–0·584 mm. in breadth, being a little wider anteriorly. The oviduct arises as an ovicapt, 0·017 mm. in diameter, from the posterior side of the isthmus near the centre instead of to one side as in the previous species (Text-figs. 30, 32). It passes backwards, forming almost immediately a short loop into the forward curve of which opens the vagina (Text-fig. 30). The vagina is very long, much longer than in *E. brachysoma*, and takes a different course. From the genital atrium it passes backwards and along the right side of the ovary as far as the isthmus (Text-figs. 30–32, 36–38). It then turns forwards, ventrally, and runs towards the genital atrium forming a loop, 0·020–0·026 mm. in diameter, which is a constant feature and which may be equivalent to the loop which passes around the cirrus-sac in the former species. This initial loop is, in both species, equal in length to the cirrus. In *E. brachysoma*, owing to the posterior position of the cirrus-sac, the vagina must encircle it, whereas in *E. affine* it can pursue an unimpeded course backwards behind the cirrus-sac. Near the genital atrium the vagina turns backwards again, becoming slightly narrower in diameter and thrown into coils lying in the ventral half of the proglottid. Between the lobes of the ovary it straightens, turns dorsally to pass above the isthmus where it enlarges to form a receptaculum seminis 0·039 × 0·042 mm. It then narrows again abruptly, forming a duct 0·010 mm. in diameter which opens into the oviduct (Text-figs. 30, 32, 38). This sudden narrowing of the vagina was apparent, also, in *E. brachysoma*, but in that case there was no notable swelling to form a receptaculum seminis. The vagina is surrounded along most of its length by a layer of cells which are probably glandular. Having received the vagina the oviduct turns backwards in the middle line and forms an elongated U-shaped slightly undulating loop between the lobes of the ovary (Text-fig. 30) which, shortly before the bend of the U, receives the median yolk duct (Text-figs. 30, 39). The bend of the U is surrounded by Mehlis's gland, 0·102 × 0·079 mm., which lies between the lobes of the ovary and not behind them as in the previous species. The oviduct emerges dorsally as the uterine duct measuring 0·008 mm. in diameter which passes forwards dorsally to the vagina and ovary but ventral to the vas

Text-figs. 31–35. *Echinobothrium affine* Diesing

Text-fig. 31. Horizontal section through ventral half of mature proglottid showing the vas deferens entering the cirrus-sac, the uterus, vagina and yolk follicles.

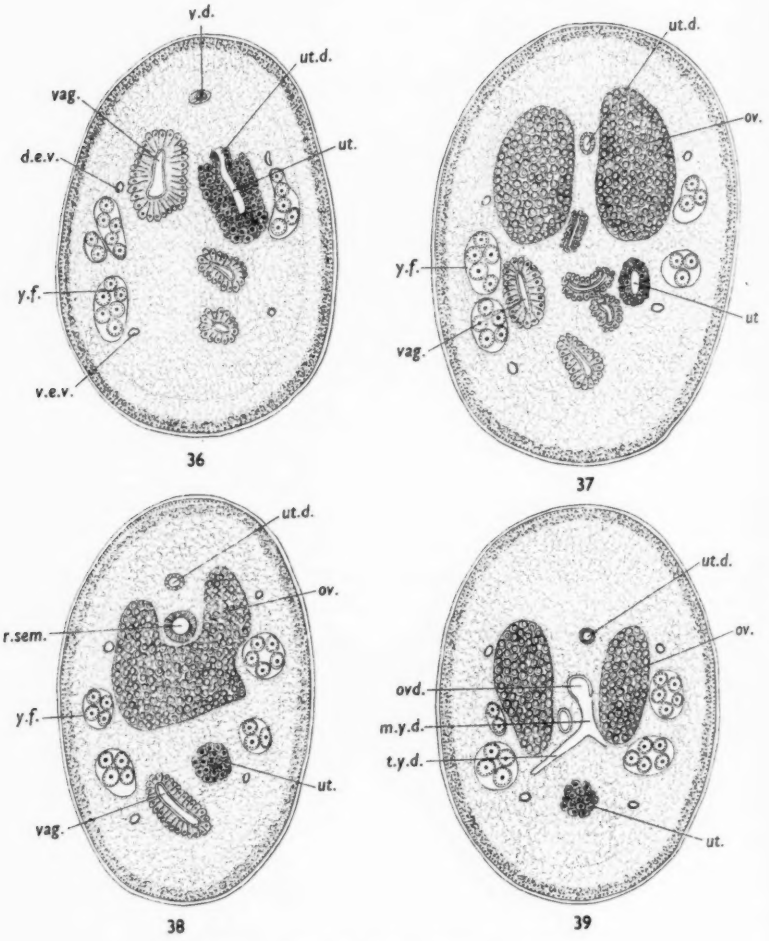
Text-fig. 32. Horizontal section through dorsal half of mature proglottid showing the vas dererens, ovary, vagina, ovicapt and uterine duct.

Text-fig. 33. Oocyte and two yolk cells, surrounded by transparent tube, from uterine duct.

Text-fig. 34. Chain of rounded eggs in transparent tube within uterine duct. Capsule not yet formed.

Text-fig. 35. Fully formed eggs, in chains in transparent tube, removed from uterus. Pronuclei and polar bodies present, capsule with appendage, yolk cells now without shell globules.

deferens and opens into the dorsal side of the uterus in the neighbourhood of the cirrus-sac (Text-figs. 30–32, 36, 37–39). The uterus is, at first, a short narrow tube lying dorsal to and behind the cirrus-sac. As the proglottid matures the uterus extends forwards in the middle line, or just to one side of the middle line, curving



Text-figs. 36–39. *Echinobothrium affine*, Diesing

Text-fig. 36. Transverse section through proglottid showing the uterine duct entering the uterus, the vagina, yolk follicles and vas deferens.

Text-fig. 37. Transverse section through proglottid showing the ovary, vagina, uterine duct and uterus.

Text-fig. 38. Transverse section through proglottid showing the isthmus of the ovary, the uterine duct, vagina and part of uterus.

Text-fig. 39. Transverse section through proglottid, showing the ovary, the median yolk duct entering the oviduct, the uterine duct and part of uterus.

around the cirrus-sac and lying ventrally to the testes and also backwards dorsally and usually to the left side of the ovary (Text-figs. 30, 31). In this condition it is still empty but as eggs pass into it it expands into a sac which fills the central part of the proglottid (Pl. 3, figs. 2, 6).

There are two rows of 45–54 yolk follicles extending along the length of the proglottid on either side (Text-figs. 30–32, 36–39; Pl. 3, figs. 2, 3). In a mature proglottid they measure 0·047 × 0·029 to 0·058 × 0·035 mm. There is a longitudinal yolk duct on either side (Text-fig. 30). The transverse yolk ducts pass towards the middle line just behind the isthmus and join to form the median yolk duct which opens into the oviduct. The yolk follicles and sometimes the yolk ducts are packed with yolk cells 0·011–0·014 mm. in diameter. As in the previous species they contain yellow shell globules around the periphery and a central nucleus.

The oocyte on entering the uterine duct has, as in *E. brachysoma*, acquired two yolk cells which become arranged in line behind it, the whole measuring 0·023 × 0·011 mm. Unlike the previous species the eggs are surrounded by a delicate transparent tube which is continuous from one egg to the next but constricted between them (Text-figs. 30, 33). As the eggs pass along the uterine duct and just in front of the level of the ovary they become rounded, measuring about 0·020 mm. in diameter, the yolk cells changing position so that with the oocyte they form, almost, a triangle (Text-fig. 34). The surrounding transparent tube expands to follow the shape of the eggs but is still constricted between them. The tube with the contained eggs passes from the uterine duct into the uterus where it coils up and eventually fills it. Shortly after entering the uterus the egg capsule is secreted, being formed, presumably, from the yellow globules in the yolk cells. At first it is transparent but later stains deeply with malachite green as do the hooks and the yolk cells. The fully formed egg is spherical, measuring 0·015–0·016 mm. in diameter and has a long appendage, 0·076 mm. in length, curled at the apex (Text-fig. 35). The transparent tube is still present around the eggs but is now only slightly constricted between them; some of the appendages may even penetrate through it. The eggs remain in this tube while in the uterus, giving the very characteristic appearance to the gravid proglottid in this species (Pl. 2, figs. 2, 6). It is not present in *E. brachysoma*. It may be formed, possibly, by Mehlis's gland or by the eggs themselves.

The development of the eggs has not been followed but, as they enter the uterus, male and female pronuclei can be distinguished and also what are probably polar bodies. The shell globules have disappeared from the yolk cells (Text-fig. 35). This is similar to the condition found in *E. brachysoma*.

DISCUSSION

There has been no difficulty in the identification of *E. affine*, as it can be recognized easily by the egg chain in the uterus. It differs from *E. brachysoma* in its greater size, the number of apical hooks and the number of hooks in each row on the peduncle. The cirrus-sac is much farther forwards than in most of the species and this, consequently, influences the course of the vagina. Euzet (1951) gave a key

for the identification of seven species of the genus *Echinobothrium* in which he bases the initial separation of *E. brachysoma* on the one hand from *E. affine* and *E. typus* on the other on the number of testes, there being as he stated 6–7 in the former and 8–10 in the latter. I find they number 6–8 and 8–14, respectively, so there is some overlap and in addition the number of testes is not necessarily constant in all proglottides in the same worm. Euzet does not include *E. rajii* Heller (1949), a form with 30–32 dorsal and ventral apical hooks, eight hooks in each row on the peduncle and sixteen testes. It resembles *E. musteli* more closely than any other species but differs from it in having no spines on the rostrum.

SUMMARY

1. *Echinobothrium brachysoma* Pintner and *E. affine* Diesing have been found in the spiral valve of *Raja clavata* L. off the coast of Britain.

2. The spiral valve is lined by tubular crypts into which the scolices of the worms are thrust, the strobila, with one gravid proglottid, being free in the lumen.

3. The functional morphology of the scolex of *E. brachysoma* has been described. That of *E. affine* appears to be similar.

4. The scolex adheres, mainly, by the apical hooks which can be raised by inner and outer elevator muscles attached to their roots and closely associated with the rostellum.

5. The rostellum can be protruded by the contraction of a dorsal and a ventral protractor muscle. Movements of the rostellum elongate the scolex in a dorso-ventral direction, forcing the apical hooks against the crypt wall and supporting them.

6. The peduncle hooks are not often embedded in the epithelium. Both series of hooks damage the epithelial lining of the crypt.

7. The remaining musculature, excretory and nervous systems are described.

8. The genitalia are essentially the same in both species. The number of testes varies from one proglottid to another in the same worm. In *E. brachysoma* the mid-ventral genital atrium is near the posterior end which affects the course of the vagina. The eggs in both species include two yolk cells which are similar to those of the Digenea and Pseudophyllidea.

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EXPLANATION OF PLATES 1–4

(Photomicrographs by D. Heminway Jones, M.Sc., to whom I am most grateful.)

PLATE 1

Echinobothrium brachysoma Pintner

Fig. 1. Internal surface of spiral valve of *Raja clavata* L. showing openings of tubular crypts.

Fig. 2. Worms embedded in tubular crypts.

Fig. 3. Horizontal section through wall of spiral valve showing crypts in transverse section with two worms *in situ*.

Fig. 4. Transverse section through crypt and contained scolex (anterior end of rostellum).

Fig. 5. The same (middle region of rostellum).

Fig. 6. The same (anterior end of peduncle and overlapping bothridia).

PLATE 2

Echinobothrium brachysoma Pintner

Fig. 1. Scolex covered with tubular crypt, apical hooks in resting state.

Fig. 2. Scolex covered with tubular crypt, apical hooks raised and penetrating wall of crypt.

Fig. 3. Vertical section through wall of spiral valve with worm *in situ*.

Fig. 4. Vertical section through peduncle and part of crypt wall showing damage to the epithelium caused by the peduncle hooks.

Fig. 5. Horizontal section through scolex, *in situ*, showing protractor muscle of rostellum.

PLATE 3

Fig. 1. *Echinobothrium brachysoma* Pintner.

Fig. 2. *E. affine* Diesing.

Fig. 3. *E. affine*, mature proglottid ('squash' preparation).

Fig. 4. *E. affine*, cirrus-sac ('squash' preparation).

Fig. 5. *E. brachysoma* showing cirrus evaginated and clusters of eggs in the uterus ('squash' preparation).

Fig. 6. *E. affine*, gravid proglottid ('squash' preparation) showing eggs in chains.

PLATE 4

Fig. 1. *Echinobothrium affine* Diesing. Scolex in optical section showing inner and outer hook elevator muscles and rostellum.

Fig. 2. *E. affine*, showing more superficial diagonal muscles and anterior circular muscle band, lateral view.

Fig. 3. *E. affine*, apex of scolex showing eleven apical hooks.

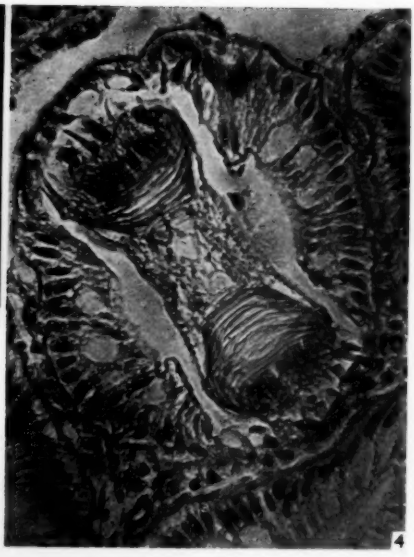
Fig. 4. *E. affine*, proglottides 5–7 showing testes.

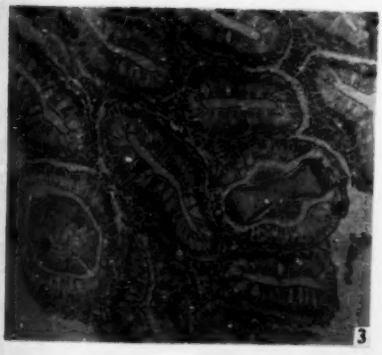
Fig. 5. *E. brachysoma*, sagittal section through scolex showing loop formed by joining of dorsal and ventral excretory vessels.

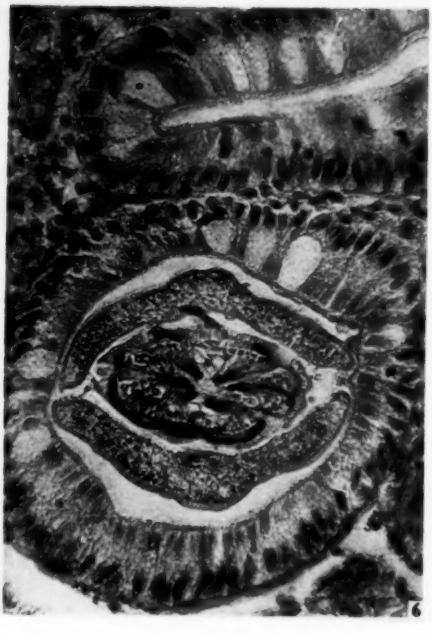
KEY TO LETTERING OF FIGURES

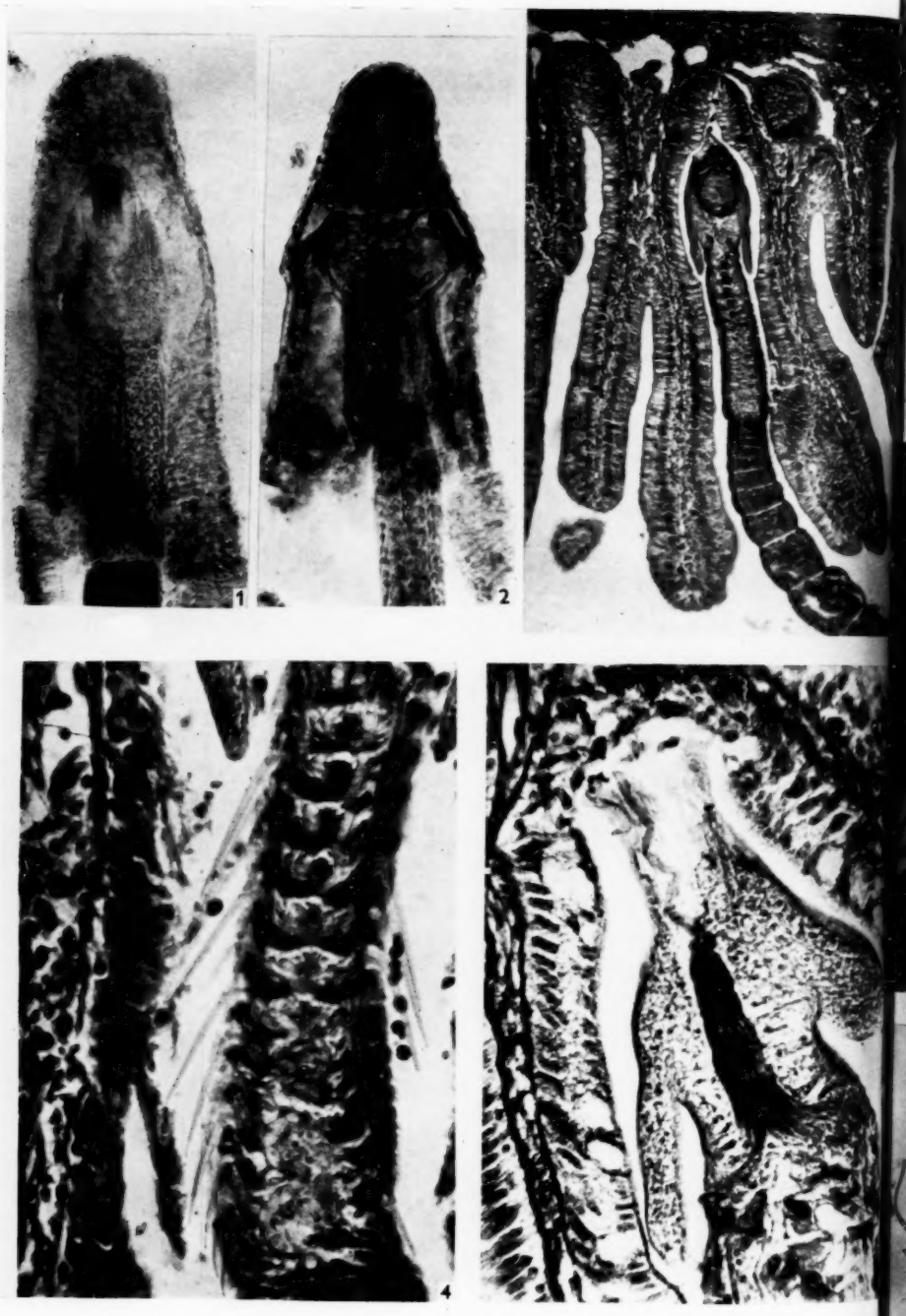
(All drawings are semi-diagrammatic)

a.c.m.	anterior circular muscle band	*ov.*	ovary
a.d.m.	anterior dorso-ventral muscles	*ovc.*	ovicapt
a.n.	anterior nerve	*ovd.*	oviduct
b.	bothridium	*p.b.*	polar bodies
bl.	blade of hook	*p.gl.*	prostate gland cells
c.	cirrus	*p.h.*	peduncle hook
c.g.	cerebral ganglion	*p.r.*	protractor of rostellum
c.m.	circular muscles	*pn.*	pronuclei
c.p.	cephalic peduncle	*r.*	rostellum
c.s.	cirrus-sac	*r.sem.*	receptaculum seminis
cu.	cuticle	*rt.*	root of hook
d.m.	diagonal muscles	*s.c.m.*	superficial circular muscles of cephalic peduncle
d.e.v.	dorsal excretory vessel		
d.v.m.	dorso-ventral muscles	*s.f.*	skeletal fibres supporting hook roots
e.	egg	*s.l.m.*	superficial longitudinal muscles
e.m.p.	elevator muscles of peduncle hook	*t.*	testis
f.	fold	*t.m.*	transverse muscles
g.a.	genital atrium	*t.m.r.*	transverse muscles of rostellum
h.e.i.	inner hook elevator muscles	*t.p.r.*	tendon of protractor muscle of rostellum
h.e.o.	outer hook elevator muscles		
l.l.(1)	limiting layer of rostellum	*t.t.*	transparent tube around eggs
l.l.(2)	limiting layer of rostellum and hook elevator muscles	*t.y.d.*	transverse yolk duct
		ten.	tendon of rostellum
l.n.	lateral nerve	*ut.*	uterus
l.y.d.	longitudinal yolk duct	*ut.d.*	uterine duct
m.c.	median commissure	*v.d.*	vas deferens
m.gl.	Mehlis's gland	*v.e.v.*	ventral excretory vessel
m.m.	meridional muscles of rostellum	*vag.*	vagina
m.y.d.	median yolk duct	*y.c.*	yolk cells
nu.	nucleus	*y.d.*	yolk duct
ooc.	oocyte	*y.f.*	yolk follicle





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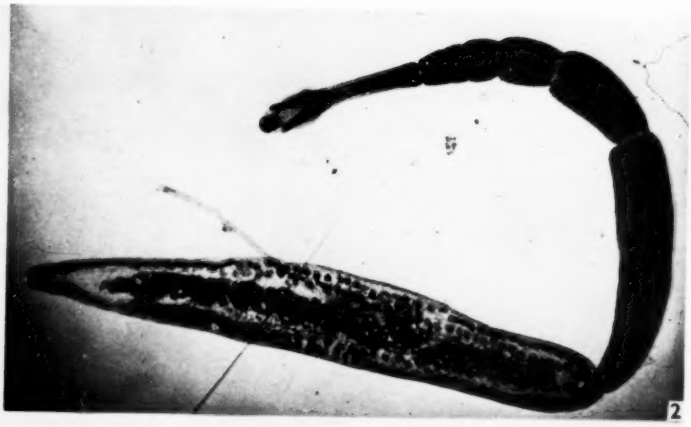

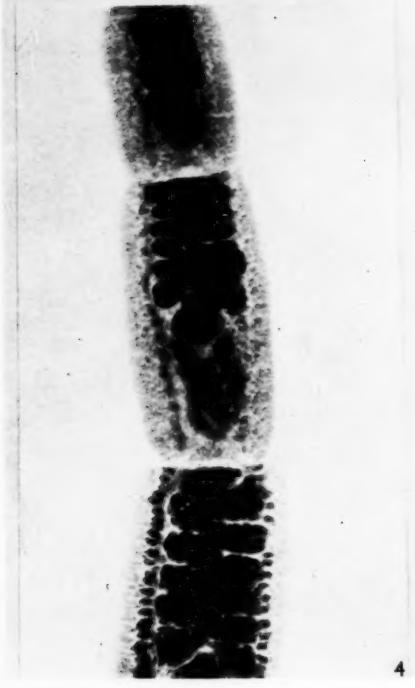

Parasitology (1961), **51**, 227–232
With 1 *plate and* 3 *text-figures*
Printed in Great Britain

Three British species of the genus *Metaradiophrya* including one new species *M. gardneri*

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(*Received* 18 *July* 1960)

INTRODUCTION

The species of Astomatous ciliates of the genus *Metaradiophrya* dealt with in the present paper inhabit the intestine of three species of earthworms. They are, together with their hosts, as follows:

Species	Host
Metaradiophrya gardneri sp.nov.	*Eisenia foetida*
M. falcifera (Stein, 1861; Heidenreich, 1953)	*Allolobophora caliginosa*
M. hovassei (de Puytorac, 1954)	*A. chlorotica*

All three species were encountered during a survey of the parasitic fauna of several earthworm species from various areas in Cardiff.

The genus *Metaradiophrya* Heidenreich (1935), is characterized by the possession of an anterior ventrally placed attaching apparatus which is connected to a supporting apparatus consisting of ectoplasmic fibres. These ectoplasmic fibres are constant in number and distribution in the different species (de Puytorac, 1954). The attaching apparatus is composed of a curved ventrally directed central spine or hook, which is part of a larger shaft lying in the right side of the cell body. In some species the apparatus may also include a smaller shaft attached to the central spine and lying in the left side of the cell body. The shape and extent of development of the attaching apparatus is also characteristic for the species. The attaching apparatus and the supporting fibres are together referred to as the cytoskeleton.

De Puytorac (1954), in his monograph on the Astomatous ciliates, made an extensive morphological and taxonomic study of the genus *Metaradiophrya* and gave some excellent descriptions of the known species.

METHODS

The hosts were dissected alive under earthworm saline (Pantin, 1946) and the ciliates were located by opening the gut along its length by a median dorsal incision. These operations were carried out on the stage of a low-powered binocular microscope and were illuminated by a strong beam of light from a microscope lamp. The ciliates present were readily seen as irridescent bodies by virtue of the

* This work was carried out at the Zoology Department, University College, Cardiff.

light which was reflected from their body surfaces while moving within the beam. They were removed by means of fine pipettes and their morphology studied while restricting their movement by cover-glass pressure. This method facilitated detailed study of the cytoskeleton of the three species. Living specimens were photographed by means of a 35 mm. reflex camera synchronized at $\frac{1}{50}$ sec. to an electronic flash unit with a rating of 220 Joules and a flash duration of approximately $\frac{1}{4000}$ sec. (Erasmus, 1958). This method was of considerable value when elucidating the detailed structure of the cytoskeleton.

DESCRIPTION

(1) **Metaradiophrya gardneri** sp.nov.

This species has been found in approximately 75 % of the specimens of *Eisenia foetida* examined. *M. gardneri*, like other members of the genus, is very active and is usually found in the anterior two-thirds of the host's intestine, where it occupies a position between the intestinal epithelium and the intestinal contents.

General morphology. *M. gardneri* has a narrow elongated body which is slightly wider at the anterior than at the posterior end (Pl. 1, fig. 1). The length varies between 150 and 345 μ, while the width varies between 45 and 60 μ in the mid-region of the body.

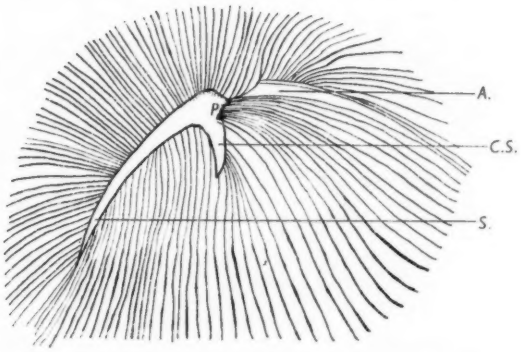
In the region of the attaching apparatus the dorsal surface of the animal is convex, while the ventral surface is concave. This region, which is often closely applied to the host's tissue by its ventral surface, is wider than the rest of the body. Thus this anterior region is between 5 and 15 μ wider than the rest of the body. The macronucleus, which is long and narrow and slightly irregular in outline (Pl. 1, fig. 1) varies between 120 and 225 μ in length. The micronucleus is a small, rod-shaped structure up to 9 μ in length, which usually lies on the right side of the body. *M. gardneri* has two rows of contractile vacuoles ranged on either side of the macronucleus. These vacuoles occur in two size groups: the smaller ones are approximately 7 μ in diameter and the larger ones between 15 and 18 μ in diameter. There are usually about twelve of the larger vacuoles present in each specimen while the smaller vacuoles are numerous.

Cystoskeleton. The attaching apparatus is typical in general form for that of the genus (Pl. 1, fig. 2; Text-fig. 1). It has the form of an inverted asymmetrical V, in which the shaft which lies in the right side of the body is much longer than the central ventrally curved spine. In this respect this species is similar to *M. gigas*, *M. lumbrici* and *M. heidenreichi*, in that the second shaft, which is developed in the left side of the cell body of some species, e.g. *M. varians*, *M. bifulta* and *M. hovassei*, is absent. This second shaft may, however, be represented by the small process on the left side of the central spine (Pl. 1, fig. 2). The size of the shaft varies only slightly: between 36 and 39 μ in length (i.e. from point to point, as it is gently curved), and it is approximately 4 μ wide where it joins the spine. The central spine varies between 12 and 18 μ in length.

There are one hundred and twenty-four ectoplasmic fibres supporting the

attaching apparatus in *M. gardneri* (Pl. 1, fig. 2; Text-fig. 1). Of these, forty-four are ventrally placed and eighty are dorsally placed. To the left side of the central spine there is a curved area of ectosarc which does not bear any ectoplasmic fibres (Pl. 1, fig. 2). This area may be up to 18 μ long and sometimes gives the appearance of being a second shaft connected to the attaching apparatus.

Taxonomic position. The general morphology and the form of the cytoskeleton exhibited by this species is typical for the genus *Metaradiophrya*. It differs in several respects from previously described members of the genus. Thus its elongated form and the size of the cell body differentiates it from all other species



Text-fig. 1. Diagrammatic representation of ventral anterior aspect of *Metaradiophrya gardneri* showing the structure of the cytoskeleton.

except *M. gigas* de Puytorac (1954), whose shape it resembles. *M. gigas*, however, is much larger than *M. gardneri*, viz. between 400 and 645 μ long as compared with 150 and 345 μ respectively. The main distinguishing feature of *M. gardneri*, however, is the cytoskeleton which contains 124 supporting fibres. This is the lowest number of supporting fibres as yet recorded for any member of the genus.

(2) **Metaradiophrya falcifera** (Stein, 1861; Heidenreich, 1935)

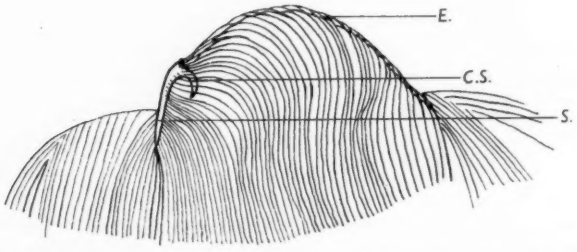
This species was first described by Stein (1861) as *Hoplitophrya falcifera* which he found occurring in a single specimen of *Lumbricus anatomicus* (*Allolobophora caliginosa*). Cépède (1910) also described it under this name. The description given by the latter author was not based upon personal observations, but on documents supplied by Maupas (Cépède, 1910, p. 405). Heidenreich (1935) created the genus *Metaradiophrya* to which this species was removed.

De Puytorac (1954) found this species infecting a single specimen of *Allolobophora caliginosa* and described the species once more. Unfortunately, however, owing to lack of material he was unable to provide a description of the quality equal to his other descriptions of species belonging to this genus. The present description is based on specimens obtained from *A. caliginosa*, where they occurred in approximately 35 % of the host animals examined.

General morphology. In shape *Metaradiophrya falcifera* is similar to *M. hovassei*

but is more rounded, while the attaching apparatus lies in a very characteristic position to the right of the cell body. The size varies between 100 and 145 μ in length by 70 and 120 μ in breadth. The macronucleus, which is irregular in outline, varies between 60 and 120 μ in length and is approximately 10 μ wide; the micronucleus is irregularly spherical in shape with a diameter of approximately 5 μ. There are up to ten contractile vacuoles arranged in two rows on either side of the macronucleus and these range in size up to 8 μ in diameter.

Cytoskeleton. The cytoskeleton of *M. falcifera* is very characteristic in the position which the attaching apparatus occupies in the body (Pl. 1, fig. 3). Unlike the arrangement in most of the other species of this genus, the central spine and the shaft to which it is connected are placed to the right side of the body. Thus the spine does not occupy a median position as in other species of the genus. This central spine is approximately 9 μ long, while the shaft which supports it varies between 15 and 18 μ in length.



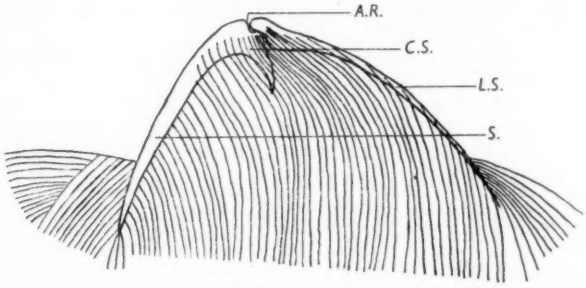
Text-fig. 2. Diagrammatic representation of ventral anterior aspect of *M. falcifera*. (The dorsal ectoplasmic fibres are not shown.)

All the previous workers have illustrated this species as having a large shaft lying on the left side of the body which is attached to the central spine and its supporting shaft. De Puytorac (1954, fig. 39) represented this second shaft as extending from the anterior tip of the central spine to near the posterior margin of the cell body. Cépède (1910, figs. 1, 2) more correctly represented the cytoskeleton as it does appear to exist. However, both of these two workers' descriptions were incorrect, for this 'second shaft' is not a solid structure but is an 'effect' produced by the overlap of the expanded anterior ends of the ventral supporting fibres. Pl. 1, figs. 3 and 4, support the structure of the attaching apparatus as represented by these two workers. Pl. 1, fig. 5, however, illustrates its correct structure. Here it is seen that the ventral fibres of the cytoskeleton expand at their anterior ends, and the majority are not connected to either the shaft or the spine, but end blindly along a curved line in the anterior region of the cell body. I have not been able to count the total number of supporting fibres in *M. falcifera* but the distribution of those in the ventral region of the animal is represented in Text-fig. 2.

(3) **Metaradiophrya hovassei** de Puytorac (1954)

M. hovassei was found by de Puytorac in the intestine of *Eisenia loonbergi*, while I have found it in approximately 65 % of the specimens of *Allolobophora chlorotica* examined.

This species (Pl. 1, fig. 6), has been adequately described by de Puytorac. In size it varies between 120 and 180 μ in length by 80 and 90 μ wide. The attaching apparatus which has a well-developed second shaft lying in the left side of the cell body is supported by a total number of 178 supporting fibres. One feature which de Puytorac did not mention is that this second shaft appears to be articulated with the other two elements of the attaching apparatus at the apex where these



Text-fig. 3. Diagrammatic representation of ventral anterior aspect of *M. hovassei*. (The dorsal ectoplasmic fibres are not shown.)

two meet (Pl. 1, fig. 7; Text-fig. 3), and is not directly continuous with them. This articulated shaft lying in the left side of the cell body is the longest of the attaching elements, and varies between 36 and 42 μ in length. The central spine varies between 10 and 15 μ in length, while the supporting shaft lying in the right side of the cell body varies between 27 and 33 μ in length.

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EXPLANATION OF PLATE 1

Fig. 1. Living specimen of *Metaradiophrya gardneri* viewed from the ventral surface. The macronucleus is seen as the broad dark band extending through nearly the whole length of the cell. × 350.

Fig. 2. Detail of the cytoskeleton of *M. gardneri*. Note the attaching apparatus and the small process on the left side of the central spine, and the clear area to the left of this small process which does not bear any ectoplasmic fibres. × 1350.

Fig. 3. Living specimen of *M. falcifera* viewed from the ventral surface. Note the attaching apparatus which is displaced to the right side of the cell body, and the 'apparent' shaft lying in the left side of the cell body. Note also the contractile vacuoles on either side of the cell body. The macronucleus and micronucleus are just discernable in this photograph. × 270.

Fig. 4. Detail of attaching apparatus of *M. falcifera* consisting of the small right shaft and central curved spine. The focus is such that the ends of the ventral supporting fibres appear to merge, giving the appearance of a second shaft lying in the left side of the cell body. × 705.

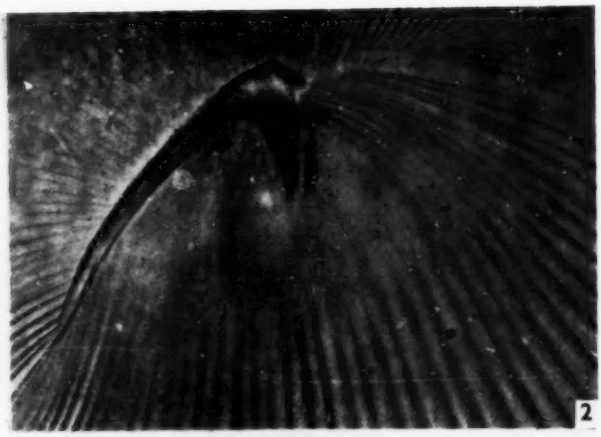
Fig. 5. Detail of the same specimen as in fig. 4, but at a different focus, showing the expanded anterior ends of the ventral supporting fibres. × 705.

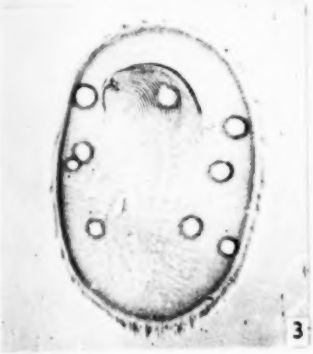
Fig. 6. Living specimen of *M. hovassei* showing the attaching apparatus with a well-developed left shaft. Note the large central macronucleus and the two rows of contractile vacuoles which appear as dark patches on each side of the macronucleus. × 400.

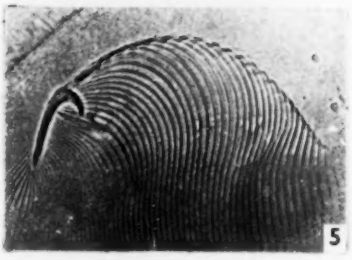
Fig. 7. Detail of attaching apparatus of *M. hovassei* showing how the left shaft is articulated with the other two elements of the apparatus. × 835.

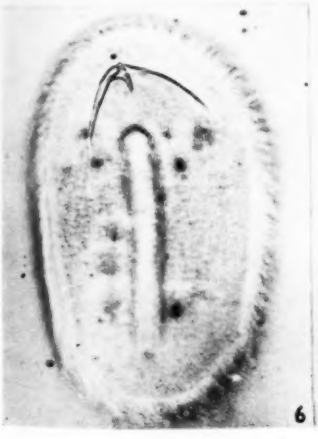
KEY TO LETTERING OF TEXT-FIGURES

A. Clear area of ectosarc which does not bear any ectoplasmic fibres.
AR. Region of articulation of left shaft with rest of attaching apparatus.
C.S. Central spine.
E. Expanded anterior ends of ectoplasmic fibres.
L.S. Left shaft of attaching apparatus.
P. Small process on left side of central spine.









B. REES

(*Facing p.* 232)

Parasitology (1961), **51**, 233–236
With 3 text-figures
Printed in Great Britain

Trematodes of Fishes from the Red Sea

10. On three new Cryptogonimidae including two new genera

By H. F. NAGATY and Tahia M. ABDEL AAL
Department of Parasitology, Faculty of Medicine, Ein-Shams University, Abbassia, Cairo, U.A.R.

(*Received* 27 *July* 1960)

The three trematode specimens described in this paper were collected by the senior author at the Marine Biological Station, Ghardaga, Red Sea; they are deposited in the collections of the Department of Parasitology, Ein-Shams University, Cairo, U.A.R.

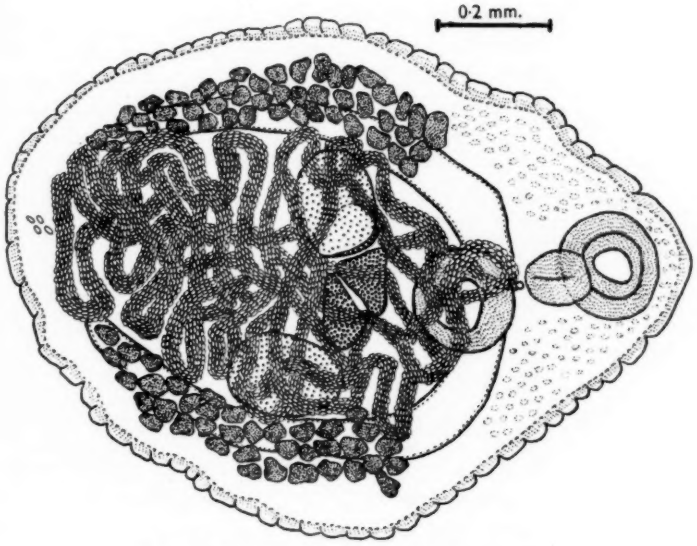


Fig. 1. *Paracryptogonimus rostratus* sp.nov.

Family CRYPTOGONIMIDAE Ciurea, 1933

Paracryptogonimus rostratus sp. nov. (Fig. 1)

One mature specimen was found in the alimentary tract of *Lethrinus rostratus*, the local name of which is 'Hebra'. It is a rather stout form, pear-shaped, measuring 1·23 mm. × 0·93 mm. having numerous glandular cells in the anterior region and provided with a thick, somewhat folded cuticle. Oral sucker subterminal, measuring 0·20 mm. × 0·21 mm. and bearing a thickened, slightly raised ridge which may indicate that the specimen had but has lost a single coronet of

circumoral spines. Ventral sucker measuring 0·18 mm. × 0·20 mm., situated at the level of the bifurcation of the gut, 0·11 mm. from the oral sucker. Prepharynx apparently absent, pharynx measuring 0·12 mm. × 0·11 mm., oesophagus short, caeca simple and terminating 0·08 mm. from the posterior extremity. Testes ovoid, confined to the intercaecal field of the mid-body the right slightly more anterior measuring 0·21 mm. × 0·17 mm. and the left 0·24 × 0·18 mm. Ovary slightly in front of the testes, comprising three wedge shaped lobes measuring 0·12 mm. × 0·08 mm. (right lobe), 0·11 mm. × 0·09 mm. (middle lobe), 0·14 mm. × 0·08 mm. (left lobe). Vitellaria comprising numerous large follicles extending from the level of the ventral sucker to the ends of the caeca, overlapping the caeca laterally. Uterus long and much convoluted, filling the intercaecal field, extending almost to the posterior extremity from the genital pore, which is median near the oesophagus. Eggs ovoid, measuring about 0·023 mm. × 0·015 mm. Other characters not determined.

Comparison. This species closely resembles *Paracryptogonimus ovatus* Yamaguti, 1952 (which was found in an unknown marine fish at Macassar, Celebes) but appears to differ (*a*) in lacking a prepharynx, (*b*) in having ovoid instead of spherical testes, (*c*) in the deep, regular folding of the cuticle, and (*d*) in having wedge-shaped instead of ovoid ovarian lobes.

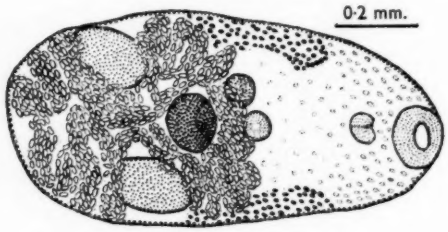


Fig. 2. *Mahrosa sargusi* gen.nov., sp.nov.

Mahrosa sargusi gen.nov., sp.nov. (Fig. 2)

A single specimen found in the alimenary tract of *Sargus noct*, the local name of which is 'Abo-nogta', displays most of the morphological features, but the caeca cannot be seen. The body is elliptical, 1·1 mm. long and 0·5 mm. broad and numerous glandular cells occur in the forebody, being most numerous in the anterior region. Oral sucker subterminal, measuring 0·14 mm. × 0·17 mm., devoid of circumoral spines. Ventral sucker much smaller than the oral sucker, 0·08 mm. diameter, situated near the middle of the body 0·3 mm. behind the oral sucker. Prepharynx 0·03 mm. long, pharynx measuring 0·08 mm. × 0·09 mm. Testes ovoid diagonally arranged in the posterior region, almost reaching the lateral surfaces; left testis, more anterior, measuring 0·20 mm × 0·15 mm., right testis 0·23 mm. × 0·17 mm., respective gonads terminating 0·27 mm. and 0·11 mm. from the posterior end of the body. Ovary ovoid, situated anterior to the testes in the third quarter of the body, measuring 0·14 mm. × 0·17 mm. Receptaculum seminis in front and on right of the ovary, behind and to the right of the ventral sucker,

measuring 0·08 mm. × 0·09 mm. Vitellaria comprising numerous small follicles arranged laterally between the levels of pharynx and ovary, mainly in the second quarter and the first part of the third quarter of the body. Transverse vitelloduct situated at the level of the ovary. Uterus long and convoluted, its folds filling the body behind the ventral sucker, overlapping the margins of the testes. Eggs small and ovoid, measuring about 0·014 mm. × 0·007 mm. Other characters not ascertained.

Comparison. This form seems to be most closely allied to the genus *Siphoderoides* Manter, 1940, but (*a*) the ventral sucker is far removed from the oral sucker, (*b*) a gonotyle having a transverse aperture is apparently non-existent, (*c*) the testes are more diagonally arranged, (*d*) the ovary is smooth instead of lobed, (*e*) the vitellaria extend nearer to the pharynx, and (*f*) the uterus extends closer to the ventral sucker.

Generic diagnosis. Body oval to elliptical, devoid of circumoral spines, having numerous glandular cells in the anterior region. Oral sucker much larger than ventral sucker. Prepharynx short, pharynx broader than its length. Testes two, lateral, diagonal, post-equatorial. Cirrus pouch absent. Ovary median, entire. Receptaculum seminis antero-lateral to ovary. Vitellaria follicular, extending laterally from level of posterior border of pharynx to level of ovary. Uterine coils filling the hind-body behind the ventral sucker. Eggs small.

Paracryptogonimoides nocti gen. nov., sp. nov. (Fig. 3)

One specimen found in the alimentary tract of *Sargus noct.* Body plump, somewhat rounded, 0·87 mm. long and 0·71 mm. broad, provided with thick cuticle. Numerous glandular cells present in anterior region. Oral sucker subterminal, measuring 0·12 mm. × 0·14 mm., its anterior border 0·09 mm. from the anterior extremity. Ventral sucker situated close behind the bifurcation of the gut and 0·08 mm. from the oral sucker, measuring 0·15 mm. × 0·18 mm. Pharynx small, spherical (0·05 mm. × 0·06 mm.), overlapping the posterior rim of the oral sucker, caeca large and extending almost to the posterior extremity. Testes large, ovoid, measuring 0·15 mm. × 0·21 mm., side by side and close together with their long axes transversely arranged, partly overlapping the caeca. Ovary having three lobes situated immediately in front of the testes; left lobe measuring 0·06 mm. × 0·11 mm., middle lobe 0·06 mm. × 0·14 mm., right lobe 0·08 mm. × 0·09 mm. Vitelline follicles fairly large, numbering 38–40 on each side of the body, approximately in the posterior region but left group more anterior than the right group, mainly extra-caecal but overlapping the outer borders of the caeca. Uterus somewhat convoluted, extending posteriorly between the testes to the ends of the caeca, slightly overlapping the testes but anteriorly not extending beyond the anterior border of the ovary. Eggs ovoid, measuring about 0·015 mm. × 0·008 mm. Other characters not determined.

Comparison. This form seems to be most closely allied to the genus *Paracryptogonimus* Yamaguti, 1934, but (*a*) the oral sucker is subterminal and is devoid of circumoral spines, (*b*) a prepharynx is absent and (*c*) a receptaculum seminis is absent.

Generic diagnosis. Body small, plump and rounded, having numerous glandular cells in the anterior region. Oral sucker subterminal, devoid of circumoral spines. Ventral sucker situated in second quarter of body. Pharynx small, caeca terminating near posterior extremity. Testes symmetrical, situated in third quarter of body, slightly overlapping intestinal caeca and separated from one another by a fold of uterus. Ovary having three lobes, pretesticular. Receptaculum seminis absent. Vitellaria having few, fairly large follicles arranged in two lateral groups extracaecal and partly overlapping caeca, extending from the level of the ventral sucker to near the ends of the caeca, mainly in the posterior half of the body. Uterus extending between the testes to the ends of the caeca.

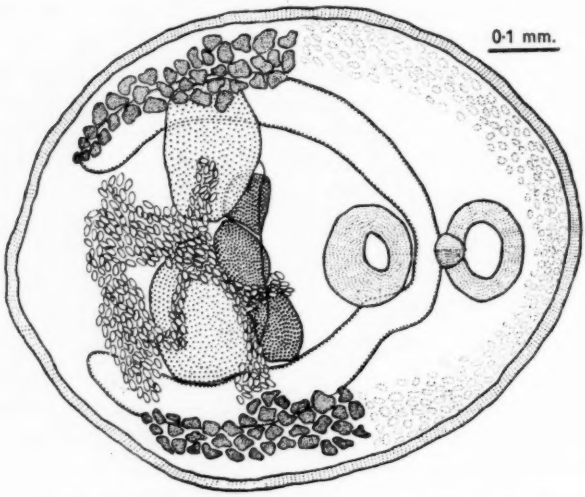


Fig. 3. *Paracryptogonimoides nocti* gen.nov., sp.nov.

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Parasitology (1961), **51**, 237–240
With 9 text-figures
Printed in Great Britain

Two new species of cryptobiotic (anabiotic) freshwater nematodes, *Actinolaimus hintoni* sp.nov. and *Dorylaimus keilini* sp.nov. (Dorylaimidae)

By D. L. LEE*
The Molteno Institute, University of Cambridge

(*Received* 10 *August* 1960)

Dr H. E. Hinton, who is working upon the larva of a chironomid, *Polypedilum vanderplanki* Hinton (1951), found in dried mud from shallow rock pools at Anara, alt. 2500 ft., about 20 miles south-east of Kaduna in Northern Nigeria, noticed that there were nematodes in this dried mud which revived when placed in water and very kindly sent me the material to examine.

The following account is taken from Hinton (1951) and describes where these nematodes and chironomid larvae were found.

> The hollows at Anara are on a granite rock about 30 feet high and nearly an acre in area. The hollows are about 18 by 9 inches and are 5–9 inches deep.
>
> On the bottom of the pools there is a layer of soil consisting of dust and fine particles eroded from the adjoining rock surfaces, as well as the remains of plants. When this layer is dried, it is one to one-and-a-half inches thick.
>
> The rainy season lasts from about March to the middle of October. The rains begin in March, and the pools fill and dry three or four times during March and April. From May until September they are kept filled and must regularly overflow. In September they dry again and may fill and dry two or three times before the rains end in the middle of October. Occasional storms that may fill the hollows occur between November and the end of February.

Dr Vanderplank, who collected the material, found that the temperature of the wet mud one afternoon in January was 40° C.

There are in fact two species of nematode in this dried mud, *Actinolaimus hintoni* sp.nov. and *Dorylaimus keilini* sp.nov., and both species revive when placed in distilled water. Not only do the larval stages of these nematodes revive but many of the adults also revive.

The nematodes in the dry mud are coiled up and have a shrivelled appearance, but when placed in water they immediately begin to swell and straighten out, and after several hours many of them begin to show signs of activity. It was found that there were 47 females and 10 males of *Actinolaimus hintoni*, 20 females and 5 males of *Dorylaimus keilini* and 133 larvae (total of both species) in 1 g. of dried mud. I have found that 9 % of the larvae revived when they were placed in water but that only 1–2 % of the adults of both species revived. Many of the adults which did not revive were found to be injured in some way. It is possible that survival would be greater in fresher soil, as that with which I am dealing was collected in October 1959. Some of this dried mud which had been kept covered with a layer of water in a test-tube for 6 months was found to contain active *Actinolaimus* and *Dorylaimus*.

* Research Fellow of Christ's College, Cambridge.

Dr Hinton also sent me some 10-year-old dried mud collected in October 1949, from dry rock pools at Vom in Northern Nigeria, and both species of nematode were found in this mud but only a very small number of them revived.

The nematodes were presumably introduced into these temporary rock pools from more permanent pools by water-beetles which leave the pools when they dry up. There are numerous broken remains of these water-beetles in the mud.

It is a well known phenomenon that many terrestrial nematodes will revive, when placed in water, after long periods during which they were kept in a dry state. Menzel (1920) reported that Spitsbergen mosses, which had been kept dry for 2 years, contained species of *Plectus*, *Dorylaimus* and *Cephalobus* which when wetted were found to be alive. Hyman (1951) states that live nematodes were obtained on wetting a sample of moss kept dried in a herbarium for $4\frac{1}{2}$ years. The larval and adult stages of certain plant parasitic nematodes are known to be extremely resistant to drying (Goodey, 1923; Corder, 1933; Steiner & Albin, 1946).

Actinolaimus hintoni sp.nov. (Figs. 1–6)

Female: 1·8–2·1 mm.; $a = 30$; $b = 4{\cdot}3$; $c = 8$; $V = 45$. (Figs. 1, 2 and 4–6.)

Male: 1·35–1·62 mm.; $a = 26$; $b = 3{\cdot}3$; $c = 76$; $T = 73$. (Fig. 3.)

Lip region about one-third that of neck base, set off by slight depression. Amphid aperture slits about one-half as long as head width. Pharynx armed with four large onchia (Fig. 1). Guiding ring double. Spear 25μ long and 3μ wide; the aperture occupying about one-third its length. Oesophagus expanded slightly anterior to middle. Intestinal cells with many bright brown granules. Prerectum length of female twice body width. Male prerectum extending past anterior supplements; three times body width. Female tail attenuated; male tail short and rounded; supplements in two groups of six each (Fig. 3); posterior supplements begin 0·080 mm. from anus. Vulva in the form of a cross (Fig. 5).

Habitat. Shallow rock pools in Northern Nigeria.

This nematode is named after Dr H. E. Hinton, who very kindly sent me the material.

Figs. 1–6. *Actinolaimus hintoni* sp.nov.

Fig. 1. Anterior end of female (lateral view).

Fig. 2. Tail of female (lateral view).

Fig. 3. Posterior end of male (lateral view).

Fig. 4. Anterior end of female (dorsal view).

Fig. 5. *En face* view of vulva.

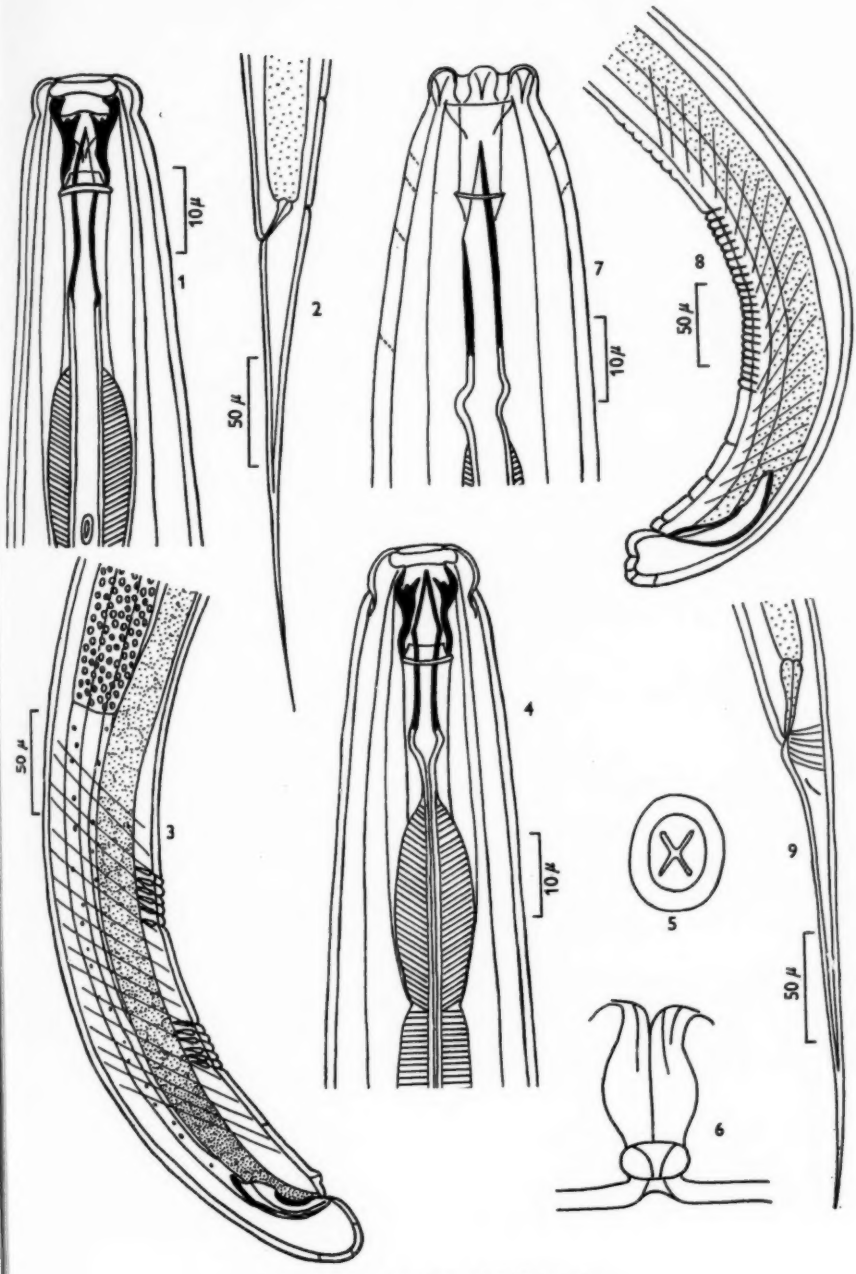
Fig. 6. Lateral view of vulva and ovijector.

Figs. 7–9. *Dorylaimus keilini* sp.nov.

Fig. 7. Anterior end of female (lateral view).

Fig. 8. Posterior end of male (lateral view).

Fig. 9. Tail of female (lateral view).



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Dorylaimus keilini sp.nov. (Figs. 7–9)

Female: 2·2 mm.; $a = 42$; $b = 4{\cdot}0$; $c = 12$; $V = {}^{11}45^{18}$. (Figs. 7, 9.)

Male: 2·13 mm.; $a = 39$; $b = 3{\cdot}7$; $c = 98$; $T = 70$. (Fig. 8.)

Lips distinct and set off by slight depression. Amphid aperture two-thirds as long as head width. Spear twice as long as head width; the aperture occupying almost half its length. Guiding ring single. Oesophagus enlarged slightly posterior to middle. Intestinal cells with many brown granules. Prerectum length five times, rectum length twice, anal body width. Ovaries reflexed one-third their length. Female tail attenuated; male tail rounded, as long as anal body width; twenty-four supplements, contiguous, beginning 0·075 mm. from anus (Fig. 8); about six pairs of subventral papillae slightly anterior to supplements. Vulva longitudinal.

Habitat. Shallow rock pools in Northern Nigeria.

This nematode is named after Professor D. Keilin who has always taken a keen interest in the subject of latent life and who introduced the term 'cryptobiosis' (Keilin, 1959).

I wish to thank Dr P. Tate and Professor D. Keilin for their advice and encouragement, and Dr H. E. Hinton of Bristol for supplying the material and for his constant interest.

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Parasitology (1961), **51**, 241–256
With 11 *text-figures*
Printed in Great Britain

New species of Near Eastern agamid scale-mites (*Acarina, Pterygosomidae*) with notes on the developmental stages of *Geckobia hemidactyli* Law., 1936

By K. M. JACK

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(*Received 2 March* 1960)

The species of *Pterygosoma* described in the present work were taken from lizards in the collections of the British Museum (Nat. Hist.), and my thanks are tendered to Mr J. C. Battersby and Miss Alice Grandison for so readily facilitating their collection.

I am obliged to Dr A. Loveridge for the material of *Geckobia hemidactyli* (Lawrence, 1936), comprising females, males, nymphae and a larva.

Pterygosoma sinaita sp.nov.

Female. The chaetotaxy of the dorsum is shown in Fig. 1; it resembles that of *P. inermis* (Tragardh, (1904), 1905). However, the anterior dorsal setae are more numerous, totalling 25–32 pairs, arranged in two clusters, the mesial of 17–22 and the lateral of 8–12 serrate setae. All of the remaining 5–6 pairs of dorsal setae are serrate except for 3 pairs immediately behind the anterior dorsal setae. Of the 4 pairs of peripheral setae, 3 pairs laterally are inserted near the margin while the fourth pair, more mesial, is inserted a little way in from the body margin. The peripheral setae are all apically expanded and spiculate. A single pair of eyes is present.

The genital field is mainly ventral in position (Fig. 1*b*); there being 4 pairs of ventral genital setae and 2 pairs of dorsal genital setae. Between these are 4 pairs of genital spines, 1 pair dorsal, 1 pair terminal and the rest ventral. The mouth-parts (Fig. 1*c*) are short and stout, resembling those of *P. inermis*. The mid-dorsal seta of palp segment II is a little shorter than the similar mid-dorsal seta of palp segment III. The ventral body setation is similar to that of *P. inermis* and is normal for the genus.

Length 454–488 μ; breadth 844–903 μ.

Male. The dorsal chaetotaxy is shown in Fig. 2*a*. There are 17–19 pairs of anterior dorsal setae arranged in two dense clusters, the mesial one of 12, the lateral cluster of 5–7 setae. Two or 3 pairs of peripheral setae are inserted on the lateral apices of the body and a similarly spiculate, slightly expanded peripheral seta inserted a little way in from the posterior margin of the body, nearer to the mid-line. There are 2 pairs of stout mid-dorsal setae and a further 3–7 pairs of similar setae inserted on the dorsal surface. A single pair of eyes is present.

The awl-shaped penis is anteriorly directed and measures 107–137 μ in length.

The eversible genital cone is narrow and equipped with 2 pairs of inconspicuous simple setae (Fig. 2*b*). The mouthparts are short and stout, resembling those of the female. The cheliceral shaft is subequal in length to the swollen cheliceral base. Ventral and coxal setation is as usual for the genus.

Length 220–289 μ; breadth 457–569 μ.

Nymph. A single specimen of this stage has been seen, and is shown in Fig. 2*c*. It is similar to the female in setation pattern; however, there are only 9 serrate setae in the mesial and 4 similar setae in the lateral clusters of anterior dorsal

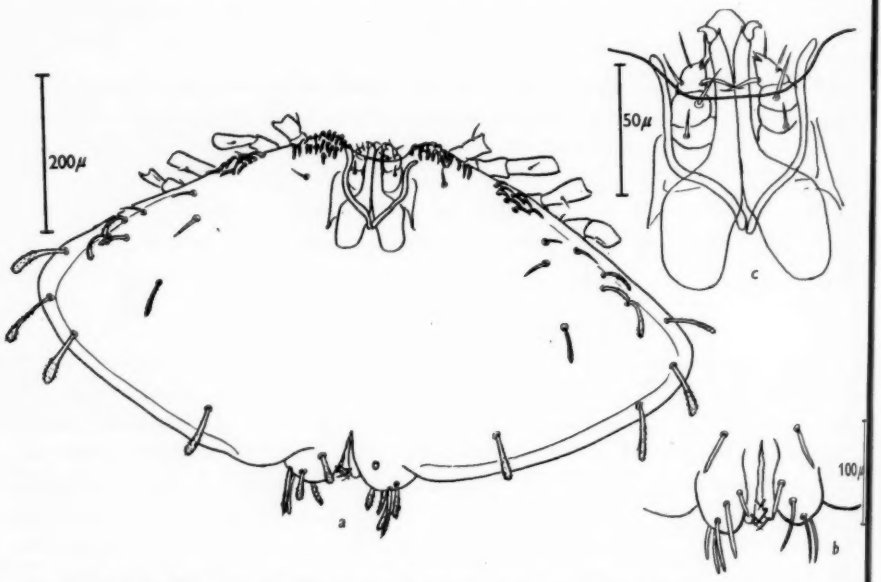

Fig. 1. *Pterygosoma sinaita* sp.nov. Female: (*a*) dorsal view of body; (*b*) genital field, ventral view; (*c*) mouthparts, dorsal view.

setae. The eyes are found just in front of this lateral cluster. In addition to this there are 7 other pairs of dorsal setae, 3 pairs of which are smooth, the rest serrate. Only 3 pairs of peripheral setae are found, 2 pairs lateral the third near to the genito-anal field.

The genital field (Fig. 2*d*) is entirely ventral in position, composed of five pairs of serrate setae which increase in length posteriorly, but are never very long. Between these are three pairs of slight genital spines, which do not intermesh across the genital fissure. Other details of ventral setation and of the mouthparts are similar to the female.

Length 241 μ; breadth 511 μ.

Distribution on the host. From beneath the ventral and lateral body scales, occasionally on the legs.

Hosts and localities

Type. Off *Agama sinaita* (B.M. No. 1953:1:7:9–10) from Jol, south of Zamabh, south-west Arabia.

Also from the same host from Serynn, Wadi Hadhramout, south Arabia; south

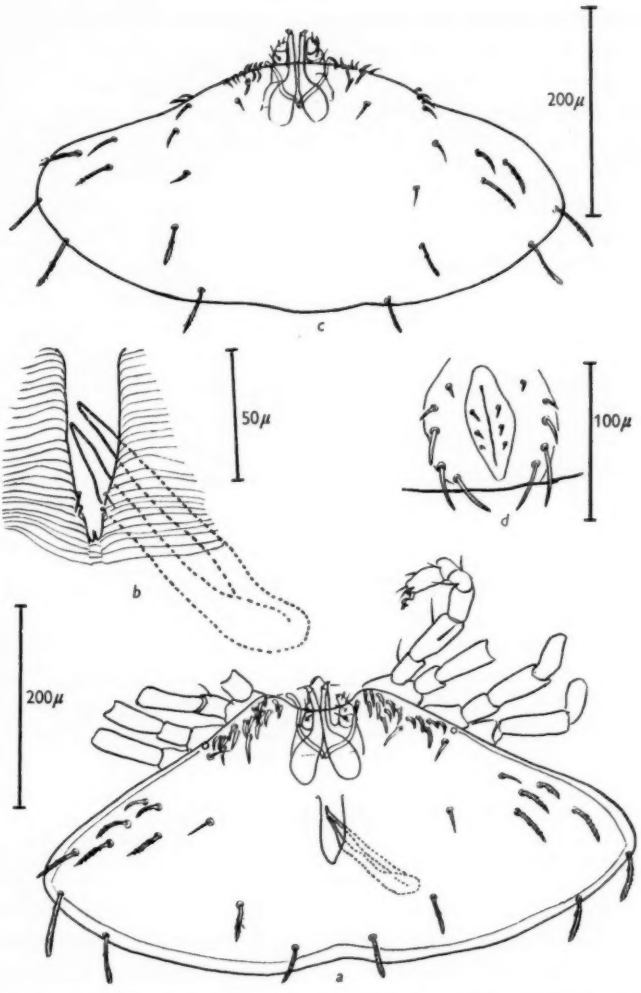

Fig. 2. *Pterygosoma sinaita* sp.nov. (*a*) Male, dorsal view of body; (*b*) male, dorsal view of genital region enlarged; (*c*) nymph, dorsal view of body; (*d*) nymph, ventral view of genito-anal region.

Hejaz, Arabia; north Jol, Hadhramout; Wadi Habal, Upper Egypt; 'Egypt'; Dead Sea; and Nuri, north Province; from *A. mutabilis* from Cirenaica, and from *A. inermis* from the Maryut District.

Pterygosoma adramitana sp.nov.

Female. The chaetotaxy of the dorsum is shown in Fig. 3*a*. There are only 6 pairs of anterior dorsal setae, arranged in two groups, the mesial group of 4 setae, the lateral group of 2 setae. All are short and apparently smooth. There are 4 pairs of apically expanded spiculate setae on the antero-lateral region of the dorsum. More posteriorly and towards the mid-line, there are 2 pairs of smaller apically expanded,

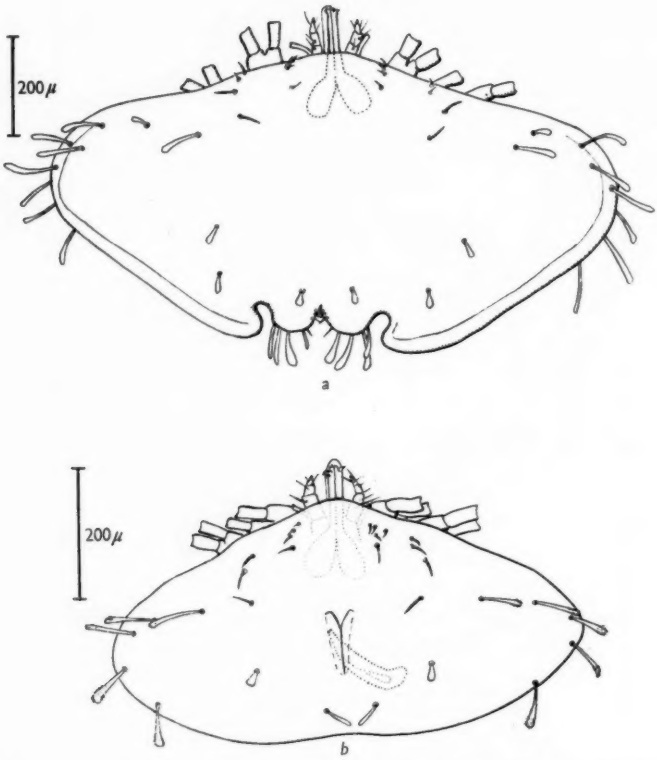

Fig. 3. *Pterygosoma adramitana* sp.nov. (*a*) Female, dorsal view of body; (*b*) male, dorsal view of body.

spiculate mid-dorsal setae. Finally there are 2 pairs of moderately long, simple, smooth setae inserted one behind the other near, and posterior, to the lateral group of anterior dorsal setae. There are 4–5 pairs of flattened, expanded, peripheral setae, the posterior 3 pairs of which are ventrally inserted the rest terminal or dorsal in position.

The single pair of dorsal genital setae are inserted a little way in from the body margin. Between and behind these setae are 3 pairs of stout genital spines. The remaining 4 pairs of genital setae are inserted ventrally and are 2–3 times as long as the dorsal pair.

The mouthparts are of the long and slender type. The chelicerae and palp setation resembles that of *P. inermis* Tragardh. The ventral setation is as usual for the genus.

Length 480–579 μ; breadth 1067–1241 μ.

Male. The body shape is similar to that of the female, but is much smaller. There are 4–5 pairs of short, spinous, anterior dorsal setae, the posterior-most of which is the longest and unserrated (Fig. 3*b*). Lateral to this group are 4 more setae, the anterior-most of which is short and serrate, the rest longer and smooth, inserted one behind the other. The remaining 4 pairs of dorsal setae are apically expanded, spiculate and longitudinally striate. Of these the 2 lateral-most pairs are the longest. There are 2 pairs of flattened, apically expanded, spiculate peripheral setae near the lateral dorsal apices. A single pair of eyes is present.

The genital cone is apparently without accessory setae, though these, being usually small, may be obscured. The penis is short and stout, measuring 97 μ in length. It is anteriorly directed as in other members of *Pterygosoma* s.str. with the exception of *P. persicum* Hirst, 1917.

The mouthparts are long and slender, another unusual feature in this genus. The chelicerae and palpi resemble those of the female, though the thumb-claw process of the palp is more than usually distinct. The ventral setation is as in the female.

Length 352 μ; breadth 705 μ.

Distribution on the host. Apparently restricted to the scales of the tail.

Hosts and localities

Type. 8♀♀ and 1♂ from *Agama adramitana* (B.M. No. 1903:3:6:1–5) from Schaf, Arabia.

Other records. From same host Hukalk, Hadhramant, south-west Arabia; and southern Hejaz, Arabia.

This species appears to be very similar to *P. inermis* Tragardh, but differs in size, the distribution of dorsal setae and in the number of genital and anterior-dorsal setae.

Pterygosoma mutabilis sp.nov.

Female. The chaetotaxy of the dorsum is shown in Fig. 4*a*. The coarsely serrate anterior dorsal setae are longer and numerous on the lateral apices of the body. The two pairs of mid-dorsal setae are stout, blunt pointed and finely serrate. There are 21–26 pairs of surprisingly stout, smooth, fine-pointed peripheral setae which are inserted in two rows, a dorsal row of 4 setae (2 near the lateral apex, 1 near the genital field and 1 midway between these), and a terminal row of 17–22 pairs.

The genital setae total 5–7 pairs which are fairly stout, short and apically flattened and slightly expanded. Between these are 3 pairs of genital spines, the posterior pair being the longest.

The ventral setation is as usual in the genus. The mouthparts are fairly short and stout, the cheliceral shaft being a little less than 1·5 times the length of the swollen

basal part of the chelicerae. The mid-dorsal seta on palp segment II is stouter but shorter than that on segment III.

Length 624–660 μ; breadth 1045–1133 μ.

Male. The chaetotaxy of the dorsum and palpi is shown in Fig. 4*b*. The serrate

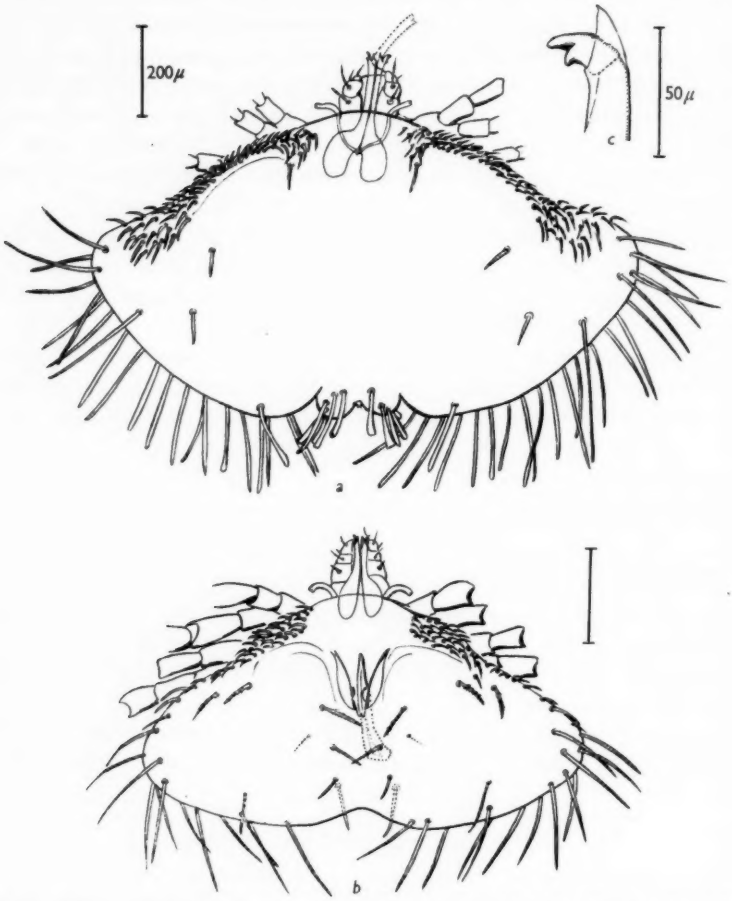

Fig. 4. *Pterygosoma mutabilis* sp.nov. (*a*) Female, dorsal view of body; (*b*) male, dorsal view of body; (*c*) female, enlarged view of tip of chelicera.

anterior dorsal setae vary in length, forming a dense cluster adjacent to the mouthparts and extending almost to the lateral apices of the body. There are 12–14 pairs of stout, smooth, blunt-pointed peripheral setae. A single pair of eyes is present.

The eversible accessory genital cone is equipped with a single pair of smooth setae. The penis is anteriorly directed. Near the genital region are three pairs of stout, serrated mid-dorsal setae. The mouthparts are short and stout, the setation of the palps being similar to that of the female except that the setae are shorter. The ventral setation is as usual for males of the genus.

Length 200–256 μ; breadth 485–509 μ.

Nymph. Two specimens were seen, but were so distorted that a figure would only be misleading. There are approximately 40 pairs of serrate anterior dorsal setae. The peripheral setae total 22 pairs, they are blunt apically, and relatively thinner and shorter than those of the female. A pair of eyes is present in the usual position. The genital field has 4 pairs of stout, blunt, serrate setae, no genital spines have been observed. The mouthparts are short and stout, resembling those of the male. Ventral setation is as usual.

Length 397 μ; breadth 676 μ.

Distribution on the host. Beneath the ventral and lateral body scales.

Hosts and localities

Type. Off *Agama mutabilis* (B.M. No. 1954:1:5:68–9) From Gebel-es-Soda, Tripolitania.

Also from *A. pallida*, Suez and same host from Beltim, between Rosetta and Damielie; from *A. jayakari* from Qatar, south Arabia; Shagra, Qatar Peninsula; from *A. inermis* from Maryut District.

Pterygosoma singularis sp.nov.

Female. The setation of the dorsal surface is shown in Fig. 5*a*. The numerous anterior dorsal setae are stout, coarsely serrate, blunt-pointed and, in the lateral region, apically expanded. The 2 pairs of mid-dorsal setae are dissimilar, the anterior pair, inserted far forward close to the anterior dorsal setae, but distinguishable from these by their slender, fine-pointed, faintly serrate form. The posterior pair are longer, apically expanded and finely spiculate. The 10 pairs of peripheral setae are all expanded and flattened at the tip and spiculate. One pair, inserted dorsally, is situated near the genital field, the rest are inserted laterally, 4 pairs dorsally the rest ventrally. No eyes have been seen.

The genital field is distinctive, there being but 1 pair of terminal genital setae which are short and paddle shaped. Between these is a conspicuous pair of genital spines.

The mouthparts are long and slender, the chelicerae measuring 227–240 μ long, the palpi are slender (Fig. 5*b*), the palp tarsus being more elongate than is usual for this genus of scale-mite.

The ventral body setation is as usual for the genus, as is the coxal setation. Tarsus I is unusual in having 2 pairs of plumose setae behind the claw instead of the more usual 1 pair (Fig. 5*c*).

Length 422–569 μ, mean 477 μ; breadth 767–932 μ, mean 839 μ.

Hosts and localities

Type. Off *Agama colonorum* (B.M. No. 1912:5:26:4–6) from Kitim, British East Africa.

Pterygosoma caucasica sp.nov.

Female. A large mite of unusual body shape (Fig. 6*a*). There are approximately 20 pairs of anterior dorsal setae, those inserted near to the mid-line are weakly serrate and blunt-pointed but towards the lateral margins they are more obviously serrate, blunt-pointed or slightly expanded at the tip. The 2 pairs of mid-dorsal

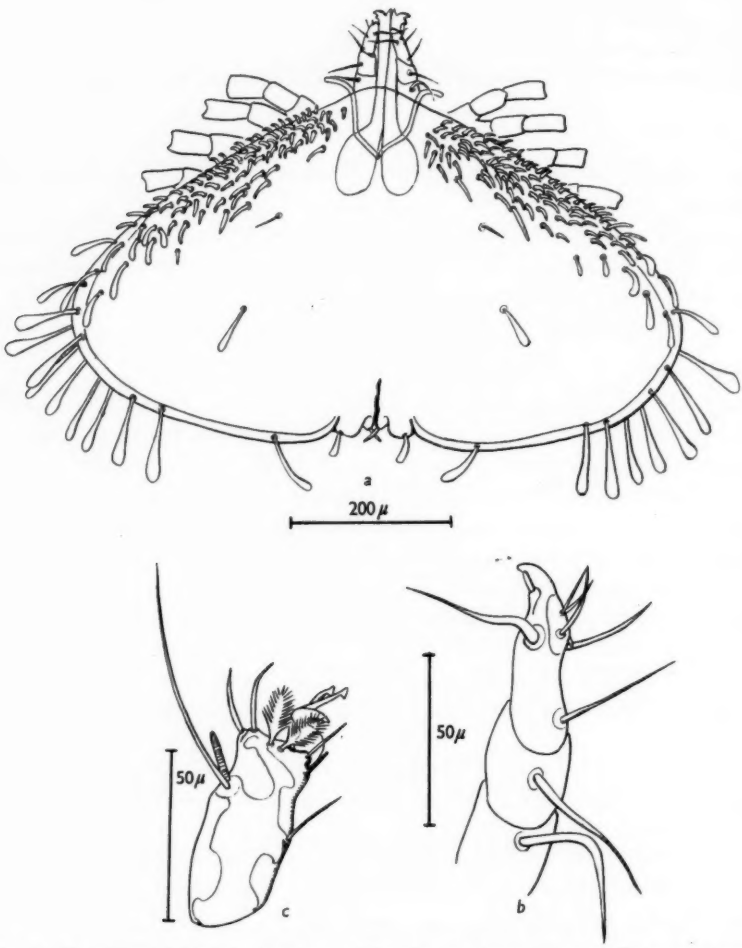

Fig. 5. *Pterygosoma singularia* sp.nov. Female: (*a*) dorsal view of body; (*b*) dorsal view of right palp; (*c*) dorsal view of left tarsus I.

setae, the 2 pairs of spiculate genital setae and the 18–22 pairs of spiculate peripheral setae, are all slightly flattened and expanded at the tip. No eyes have been observed. The genital slit is ventral in position and is equipped with 4 pairs of stout, blunt genital spines, near which is a single pair of weakly expanded, short setae.

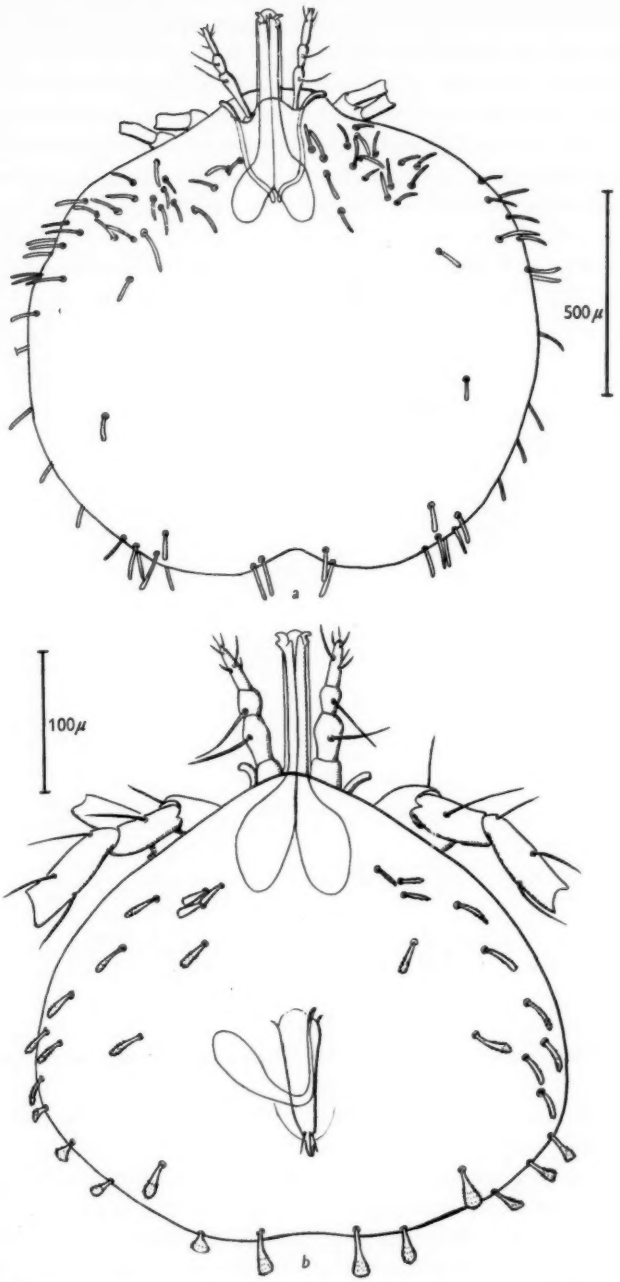

Fig. 6. *Pterygosoma caucasica* sp.nov. (*a*) Female, dorsal view of body; (*b*) male, dorsal view of body.

The remaining setae of the ventral surface follow the usual pattern for this genus, the posterior 2 pairs are somewhat expanded and faintly spiculate.

Length 847–1019 μ; breadth 1163–1209 μ.

Male. The adult male (Fig. 6*b*) is similar in chaetotaxy to the immature females to be described. There are only 5–6 pairs of widely spaced, coarsely serrate anterior dorsal setae. The 2 pairs of spiculate mid-dorsal setae, the 8 pairs of spiculate peripheral setae and the setae on the antero-lateral regions of the body are all apically expanded and flattened. One of the posterior peripheral setae is inserted rather

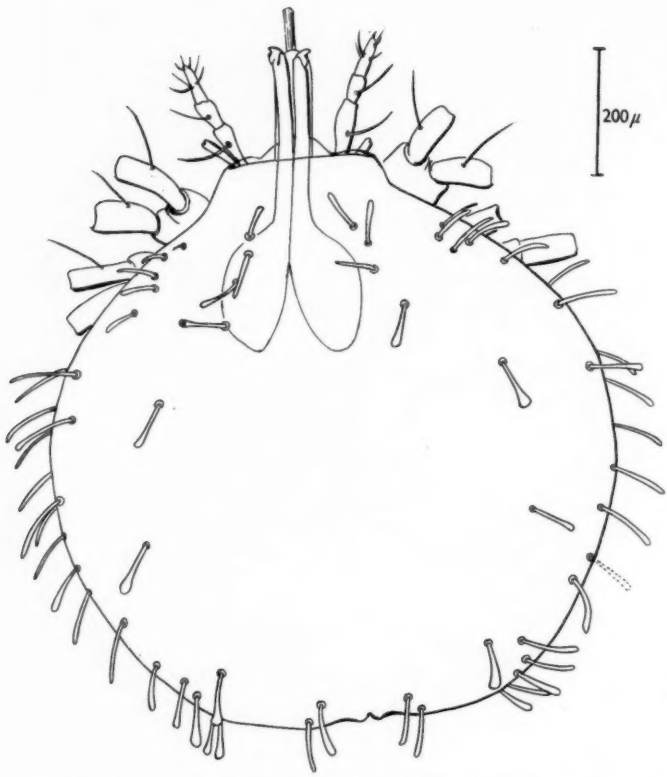

Fig. 7. *Pterygosoma caucasica* sp.nov. Deutonymph, dorsal view of body.

more on the dorsum and another more on the venter than the rest of the peripheral setae. No eyes have been observed.

The genital apparatus is situated to the posterior of the body and is of the eversible type found in other males of *Pterygosoma* s.str. The retracted genital cone is equipped with a single pair of short, slender, fine-pointed setae. The penis is recurved and so measurement of length could not be taken without dissection. There are no mid-dorsal setae behind or adjacent to the genital apparatus.

The usual 3 pairs of ventral body setae are found, the anterior pair simple and

fine, the second pair serrated and apically expanded, the third, posterior pair, inserted near to the posterior margin of the body. The coxal setation is as usual for the genus. The setation of the palpi as in the female (Fig. 6*a*).

Length 328 μ; breadth 351 μ.

Deutonymph. The chaetotaxy of the dorsum is shown in Fig. 7. It resembles that of the female, but possesses fewer anterior dorsal setae, and only 14 pairs of peripheral setae. Ventrally there are 4 pairs of setae as in the protonymph (below). The genital slit is ventral and has the 4 pairs of genital spines and the associated pair of setae as in the female. Setation of the coxal plates and mouthparts as in the female. The figured specimen shows a feeding tube similar to that of the larva of *Trombidium fuliginosum* and presumably formed in a similar manner.

Length 892–944 μ; breadth 764–771 μ.

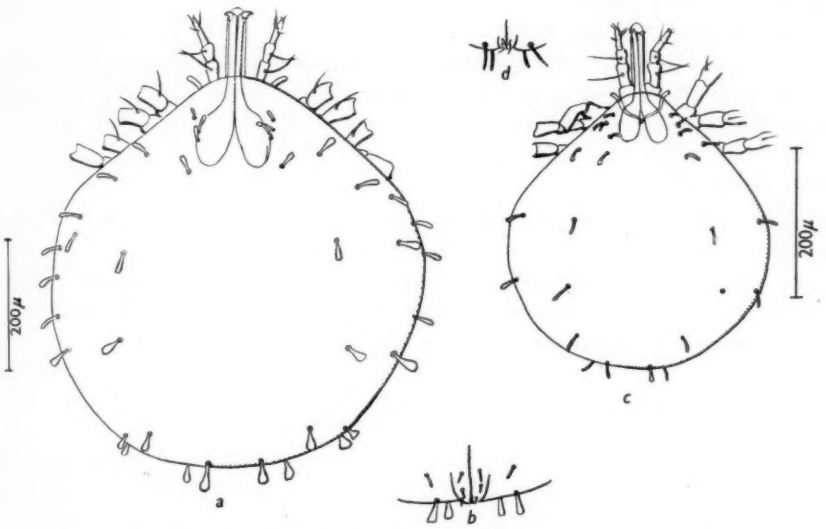

Fig. 8. *Pterygosoma caucasica* sp.nov. (*a*) Protonymph, dorsal view of body; (*b*) protonymph, ventral view of genito-anal field; (*c*) larva, dorsal view of body; (*d*) larva, ventral view of genito-anal field.

Protonymph. The dorsum is shown in Fig. 8*a*. It differs from the adult and deutonymph in having fewer setae. A total of 19 pairs of spiculate setae are found on the dorsum, 8 pairs of peripheral setae, 6–7 pairs of anterior dorsal setae and 2 pairs of mid-dorsal setae. The 2 pairs of posterior-mesial setae visible from above are ventrally inserted and presumably correspond with the 2 pairs of dorsally inserted genital setae of the female and deutonymph. No eyes have been seen. The mouthparts are elongate so differing greatly from the condition usually found in the protonymphae of *Pterygosoma* s.str. The genito-anal field is ventral as in female and deutonymph. In addition to the 2 pairs of genital setae mentioned above there are 3 pairs of genital spines which do not intermesh across the fissure, and a

further pair of genital setae (Fig. 8*b*). The rest of the ventral setae and the setation of the coxae is as usual for the genus.

Length 576 μ; breadth 548 μ.

Larva. The body is pyriform, its chaetotaxy is shown in Fig. 8*c*. The anterior dorsal setae are represented by 3 pairs of setae (on one side one of these setae is duplicated). Behind these setae are 2 pairs of longitudinal rows of similar setae, the lateral row of 3 setae, the mesial row of 5 setae. Ventrally, near the posterior margin, is a similar pair of setae. All of these setae are spiculate and more or less apically expanded. No eye has been seen.

The chelicerae are elongate, the cheliceral shaft being twice as long as the swollen basal part. The palpi are long and slender, their setation as in Fig. 8*c*. The genital field, situated ventrally (Fig. 8*d*), has 3 pairs of slender genital spines in addition to the setae mentioned above. The setation of the venter is as usual for the larvae of this genus.

Length 380 μ; breadth 361 μ.

Distribution on the host. Widespread over the body, inserted between the scales, the body being left almost completely unprotected. Found on belly, tail and skin folds of the neck, ear and legs.

Host and locality records

Type. Off *A. caucasica* (B.M. No. 74:11:23:15–18) from Kornd, north of Isfahan, Persia.

Also from the same host from near Quetta; Ashkabad; Rubbarek, north Elbung, north Persia; Doab; and Bamian, north Afghanistan; and also off *Agama nupta* from Jupa, 13 miles south of Kermanshah, Persia.

Pterygosoma foliosetis sp.nov.

Female. The chaetotaxy of the dorsum is shown in Fig. 9*a*. On each side of the mouthparts is a dense cluster of apically expanded and flattened anterior dorsal setae, the lateral-most of which are longer than the rest. Lateral to these setae are 9–10 pairs of yet longer, leaf-like setae, the surface of each being covered with vein-like striations (Fig. 9*b*). The 10–20 pairs of dorsally inserted peripheral setae and the 4 pairs of dorsally inserted genital setae are similarly patterned. There is a single pair of stout genital spines dorsally between the genital setae.

The ventral surface has the usual 3 pairs of setae, the anterior pair being the smallest. The setation of the coxal plates is normal for the genus. The mouthparts are fairly long and slender, the cheliceral shaft being about 1·5 times the length of the swollen cheliceral base. The palpi are slender and have a slender, simple, mid-dorsal seta on segments II and III.

Length 411–581 μ; breadth 803–864 μ.

Nymph. A single specimen of this stage has been seen which resembled the female in all respects with the exception of size and numbers of setae. There are only 14 pairs of peripheral setae which are more obviously spiculate than those of the female. The elongate antero-lateral dorsal setae total 8 pairs. The anterior of

the 2 pairs of mid-dorsal setae is short, blunt-pointed and obviously serrate. Only two pairs of genital or anal setae are present, 1 pair of which is inserted dorsally, the other pair ventrally. The single pair of genital spines is also ventral in position and does not project across the genito-anal fissure.

Length 237 μ; breadth 528 μ.

Distribution on the host. Rarely attached to the host, in only two cases were they found beneath a scale. Usually found on the soft skin of the axillae.

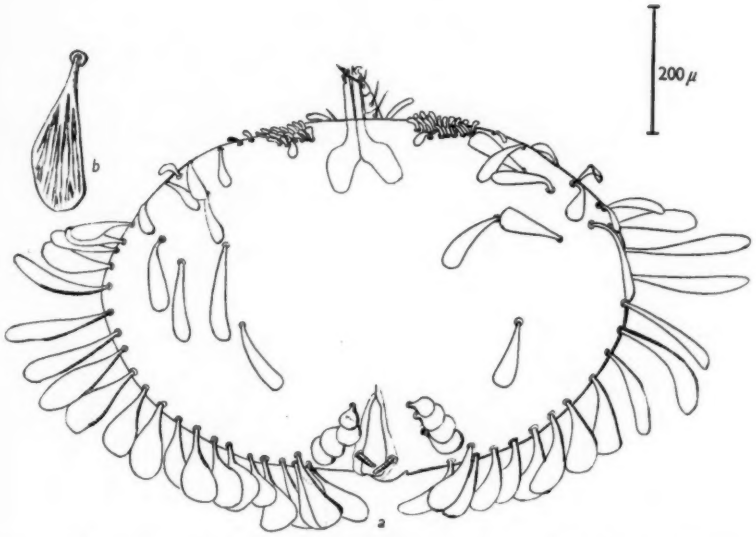

Fig. 9. *Pterygosoma foliosetis* sp.nov. Female: (*a*) dorsal view of body; (*b*) enlarged view of a patterned dorsal seta.

Hosts and localities

Type. Off *Charasia dorsalis* (B.M. No. 94:8:30:3) from Foster Hill Rise, Nilghirries, south India.

Also off the same host from Malabar, Madras; Anamallies, south India, and locality unknown.

Notes on developmental stages of Geckobia hemidactyli Law. 1936

Specimens of this mite were kindly supplied by Dr A. Loveridge. They were taken off the gecko *Hemidactylus mercatorius* Gray from between the Devil's Riding School and Table Crater, Ascension Island. Hitherto the species has been recorded only from Driefontein, Southern Rhodesia (Type locality) off *H. tasmani* and from the same host from Kutama, Southern Rhodesia and off *H. mabouia* from Lourenco Marques and from Zambesi, Belgian Congo.

Male. The body is more or less circular, the dorsal setation shown in Fig. 10*a*. The distribution and type of dorsal setae is the same as in the female, but fewer in number. The dorsal shield is inconspicuous but similar in shape to that of the

female. Eyes are inconspicuous, situated laterally to the lateral-most seta of the anterior row of dorsal shield setae.

The genital aperture is dorsal in position and is fringed by a pair of genital lobes each of which is equipped with three short, inconspicuous, spinous setae (Fig. 10*b*, from second specimen). The posteriorly directed penis measures 141 μ (Fig. 10*c*).

Fig. 10. *Geckobia hemidactyli* Law., 1936. Male: (*a*) dorsal view of body; (*b*) enlarged dorsal view of genital region; (*c*) penis.

The mouthparts are conspicuous, the chelicerae short and stout. The palp setation is similar to that of the female, except for the dorsal seta on palp segment II which is shorter and coarsely spiculate in the male.

The coxal setation differs slightly from that of the female, both in the shape and the distribution of the coxal setae. The anterior common coxa has 4 setae, the

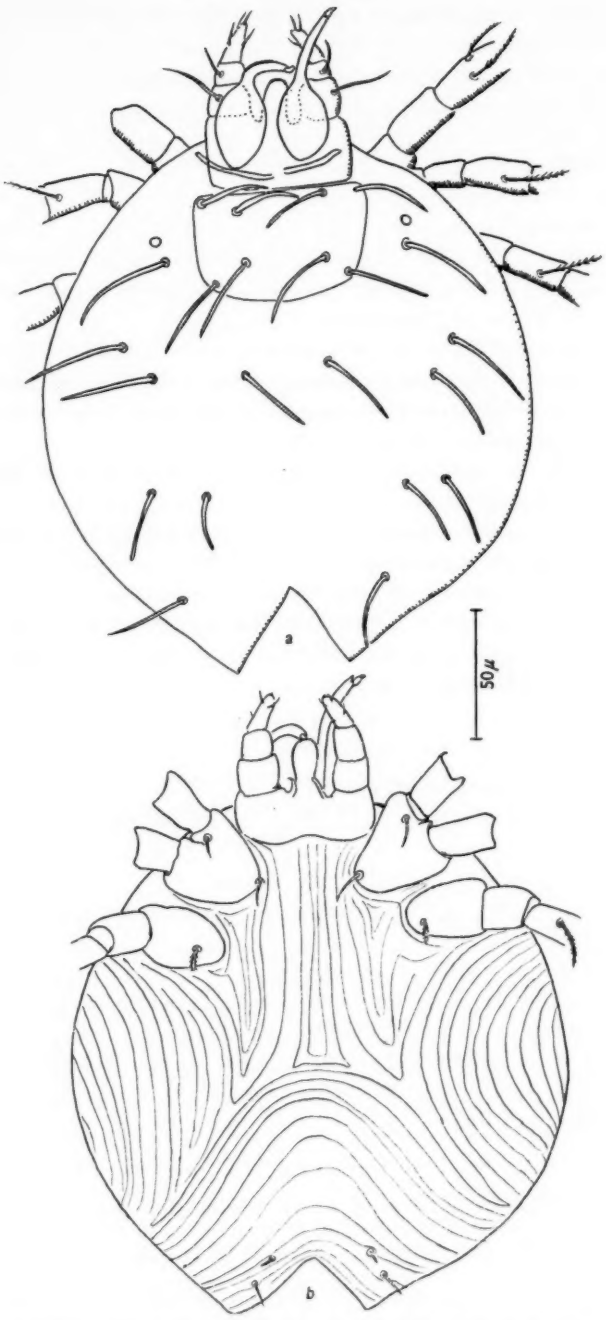

Fig. 11. *Geckobia hemidactyli* Law., 1936. Larva: (*a*) dorsal view of body; (*b*) ventral view of body.

basal seta of coxa I being elongate and smooth, the rest are shorter and spiculate though not so incrassate as in the female. The posterior common coxa has a pair of basal setae and a pair of trochanteral setae which resemble the stouter setae of the anterior common coxa. The conspicuously striate legs are short and stout, the posterior pair being the longest. The ventral surface has many setae, similar in distribution to those of the female, but fewer in number.

Length 165–192 μ; breadth 164–170 μ.

Larva. Almost circular in shape with far fewer setae than in the adult female. The dorsum with only 11 pairs of uniseriately serrate setae arranged as in Fig. 11*a*. A single pair of eyes is conspicuously placed in front of the first of the lateral row of setae as in the larvae of *Pterygosoma*.

The ventral surface (Fig. 11*b*) has 2 pairs of simple setae adjacent to the anal aperture. The anterior common coxa has 2 setae, both of which are simple and smooth, and both of which occur on coxa I. The posterior coxa has a single short, stout, spiculate seta on the base of the plate.

The mouthparts are similar in form and setation to those of the female.

Length 196 μ; breadth 185 μ.

Nymph. The body shape is similar to that of the male (Fig. 10). The distribution of setae and their shape are similar to those of the female on both dorsal and ventral body surfaces, but they are shorter and not quite so numerous. The mouthparts are identical to those of the female. The coxal setation is identical to that of the male, differing from the female in numbers of coxal setae and also in their smaller size.

Length 189–267 μ; breadth 224–268 μ.

SUMMARY

The following new species are described:

Pterygosoma sinaita sp.nov. (♀, ♂, nymph) off *Agama sinaita*, *A. mutabilis* and *A. inermis*.

P. adramitana sp.nov. (♀, ♂,) off *A. adramitana*.

P. mutabilis sp.nov. (♀, ♂, nymph) off *A. mutabilis*, *A. pallida*, *A. jayakari* and *A. inermis*.

P. singularis sp.nov. (♀) off *A. colonorum*.

P. caucasica sp.nov. (♀, ♂, deutonymph, protonymph and larva) off *A. caucasica*.

P. foliosetis sp.nov. (♀, nymph) off *Charasia dorsalis*.

Descriptions are also included of the hitherto unrecorded male, nymph and larva of *Geckobia hemidactylus* Lawrence, 1936, from *Hemidactylus mercatorius* Gray from Ascension Island.

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Parasitology (1961), **51**, 257–261
Printed in Great Britain

Synergism between coccidia parasites (*Eimeria mitis* and *E. acervulina*) and malarial parasites (*Plasmodium gallinaceum* and *P. juxtanucleare*) in the chick*

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(*Received* 12 *November* 1960)

During my study on avian malaria an outbreak of coccidiosis occurred among chicks infected with *Plasmodium juxtanucleare*. The study of this coccidial infection has shown that it was a mixed infection of three species of coccidia: *Eimeria tenella*, *E. mitis* and *E. acervulina*.

The mortality rate among the infected chicks was very high (almost all infected chicks died); therefore I decided to study the synergistic effect, if any, of the two non-pathogenic species of coccidia which were isolated during this outbreak (*E. mitis* and *E. acervulina*) on the course of infection with the malaria parasites (*P. juxtanucleare* and *P. gallinaceum*) in chicks.

The effect of mixed infections on the infected host and on each other had been studied in animals harbouring two different species of malaria parasites (Singh & Ray, 1952; Wolfson, 1945; Huff, 1937), leishmanial and malarial infections (Adler, 1954; Napier, Smith & Krishnan, 1934), bilharzial and malarial infections (Yoeli, 1956), spirochaetosis and malaria (Lion, 1939), haemobartonellosis and malaria (Hsu & Geiman, 1952). The results of these studies, as well as those of the present work, will be discussed later in the text.

MATERIALS AND METHODS

The strains of *P. gallinaceum* and *P. juxtanucleare* were the same as those previously used by the author (Al-Dabagh, 1960*a*, *b*). The coccidial parasites used (*E. acervulina* and *E. mitis*) were isolated from naturally infected chicks by the following technique: a single oocyst was picked up by a very fine 'Pasteur pipette', made especially for the purpose, under the 16 mm. objective (low power). The oocyst was then given *per os* to 3- to 7-day-old laboratory-bred chicks which were proved, by repeated faecal examination, to be free from any detectable coccidial infection. The faeces of chicks infected by the above method were collected: when a suitable number of oocysts was found in the sample, it was cultured in a solution of 1% potassium dichromate and was kept in a covered Petri dish at room temperature with daily aeration and stirring for 5–10 min. Several examinations of the culture were made before use to ascertain that the sporulation of the

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oocysts was complete, and only one kind of oocysts was present in the culture. Chicks were infected by giving them 1 c.c. of this culture *per os* with the aid of a soft fine nylon catheter and a syringe.

In the first experiment 6 chicks previously infected with *P. juxtanucleare* for 55–69 days (Table 1) were given *E. acervulina* oocysts. In the second experiment 6 chicks infected with *P. juxtanucleare* for 54–75 days (Table 1) were given *E. mitis*. In the third experiment 4 chicks infected with *P. gallinaceum* for 36–60 days were infected with *E. acervulina*. In the fourth experiment 6 chicks infected with *P. juxtanucleare* for 10 days were infected with *E. acervulina*.

RESULTS AND OBSERVATIONS

All the chicks used in the first and second experiments showed recrudescence 5–12 days (average 8 days) after being infected with the coccidial parasites. The recrudescence in these chicks continued for 13–26 days (average 18 days). Only 1 chick out of the 12 used in these two experiments died as a result of the recrudescence of *P. juxtanucleare* infection. In the third experiment all the chicks showed severe relapses 5–6 days after being infected with *E. acervulina*. Moreover, all the four relapsed chicks died 8–13 days (average 11 days) after the beginning of the relapse, due presumably to *P. gallinaceum* infection. One of the 3 chicks which were used as controls for this experiment showed a relapse and died 65 days after being infected with *P. gallinaceum*. The other two controls did not show any relapse during the whole period of observation (155 days).

The fourth experiment was designed so that the appearance of *P. juxtanucleare* in the peripheral blood and oocysts of *E. acervulina* in the faeces of infected chicks would occur at approximately the same time. All the 6 chicks used in this experiment showed approximately the same prepatent and patent periods as those of the control chicks. The mortality rate was also not affected, but the level of parasitaemia throughout the patent period of infection, particularly at the peak, was much higher in chicks harbouring the mixed infections than that seen in the control chicks (2400 parasites per 10,000 R.B.C.'s in chicks with mixed infections as compared with 1200 parasites per 10,000 R.B.C.'s in the controls).

It seems that the concomitant coccidial infection (*E. acervulina* and *E. mitis*) is capable of causing a recrudescence in chicks infected chronically with *P. juxtanucleare*. It also causes a higher level of parasitaemia in chicks infected during the prepatent period, but it does not affect materially the length of the prepatent and patent periods or raise the mortality rate in the chicks harbouring mixed infections. The coccidial parasites (*E. acervulina*) have induced severe fatal relapses in chicks with latent *P. gallinaceum* infections.

The pathological lesions observed in the internal organs (except the intestines) of chicks harbouring the mixed infections are generally of the same severity, magnitude and distribution as those observed in chicks infected with the malaria parasites alone. The intestines of chicks harbouring the mixed infection (particularly those infected with *E. acervulina*) may show minor pathological changes manifested by destruction of a few epithelial cells and mild intestinal catarrh which

Table 1. *Synergism between coccidia and malaria parasites in chicks*

Expt. no.	No. of birds used	Age when infected with malaria (average in days)	Species of *Plasmodium* used	Age when infected with coccidia (average in days)	Species of *Eimeria* used	No. of malaria parasites when infected with coccidia (per 10,000 R.B.C.s)	Recrudescence or relapse after (average in days)	Duration (average in days)	Level of parasitaemia reached (average per 10,000 R.B.C.s)	Remarks
I	6	5	*P. juxtanucleare*	66	*E. acervulina*	14	8	19	976	One chick died
II	6	1	*P. juxtanucleare*	66	*E. mitis*	47	7	17	1258	All recovered
III	4	3	*P. gallinaceum*	55	*E. acervulina*	—	6	11	6650	All died
IV	6	7	*P. juxtanucleare*	17	*E. acervulina*	—	6	20	2400	One died after 40 days
Controls	6	4	*P. juxtanucleare*	—	—	—	—	—	1200	One died after 45 days
Controls	3	4	*P. gallinaceum*	—	—	—	One relapsed and died after 65 days	2	7000	The other two chicks showed no relapse after 155 days of observation

are caused by the coccidial parasites used. These two species of coccidia are known to cause only minor pathological changes in the intestines of infected chicks, and only rarely prove to be fatal to chicks (Tyzzer, 1929; Tyzzer, Theiler & Jones 1932).

DISCUSSION

The effect which the parasites may exert on each other and on the host in mixed infections differs greatly, depending on the species of parasite and host under consideration. The parasites may have a synergistic effect on the development of each other, as for example the synergistic effect of the coccidial parasites *E. acervulina* and *E. mitis* (used in this study) on the malaria parasites *P. juxtanucleare* and *P. gallinaceum*. The reverse has also been proved to be true in the case of these parasites. In chicks which stopped passing oocysts of *E. acervulina* in their faeces, the oocysts reappeared when these chicks were infected with *P. gallinaceum* (the oocysts reappeared approximately at the beginning of the patent period of the malarial infection). Napier *et al.* (1934) have found that malaria increases the susceptibility of infected monkeys to leishmaniasis. Hsu & Geiman (1952) have reported the activation of latent *Haemobartonella muris* infection in white rats by *P. berghei*. They have also noticed that the high degree of polychromatophilia caused by *H. muris* increases the level of parasitaemia of *P. berghei* in the peripheral blood of infected rats, hence a higher mortality rate results (50% as compared with 13·8% among *H. muris*-free rats). They further believe that the synergistic effect of *P. berghei* on haemobartonellosis of the white rats may be due to the blockage of the reticulo-endothelial system of the rats, which results from the malarial infection. Yoeli (1956) has noticed that a concomitant infection of *Schistosoma mansoni* and *P. berghei* in the same vole (*Microtus guentheri*) deprives the host, in many cases, of its capability of suppressing or eliminating the malarial infection. It also increases the number of chronic malarial infections among the infected voles. He has also observed the same thing among splenectomized voles. He was, however, unable to determine the exact mechanism responsible for such interference. Therefore he assumed that the altered reticulo-endothelial system and the marked increase in its phagocytic activity caused by bilharziasis might have affected the course of the malarial infection.

The parasite may be capable of making the host less susceptible to infection by another parasite or it may suppress its development. Singh & Ray (1952) have found that *P. cynomolgi* suppresses the development of *P. inui* in monkeys, except when the animals are splenectomized. Adler (1954) has found that golden hamsters (*Mesocricetus auratus*), previously infected with a virulent strain of *Leishmania infantum*, are less susceptible than uninfected hamsters to *berghei* and *rodhaini* malarias. He therefore concluded that the infection of the golden hamsters with leishmaniasis confers marked protection against *P. berghei* and *P. rodhaini*. One of the two parasites associating in a mixed infection may not affect the course of the other. Adler (1954), for example, has found that *P. berghei* in golden hamsters apparently does not inhibit the development of *L. infantum*. Lion (1939) has observed that an infection with *Spirochaeta gallinarum* does not influence the

resistance of fowls to *P. gallinaceum*. Huff (1937) has found that the reproduction of *P. cathemerium* and *P. relictum* is not affected by the fact that they were studied in a single host (robin, *Turdus migratorius migratorius*). Wolfson (1945) has found no antagonism between *P. cathemerium* and *P. lophurae* in experimentally infected ducks in which each of the two species developed independently.

SUMMARY

1. The coccidial parasites (*Eimeria acervulina* and *E. mitis*) cause a recrudescence in chicks harbouring chronic infection with *Plasmodium juxtanucleare*.

2. *E. acervulina* causes higher levels of parasitaemia in *P. juxtanucleare* infections in chicks if the coccidial infection is produced during the prepatent period of malaria, but it does not affect the length of patent and prepatent periods or raise the mortality rate among infected chicks.

3. *E. acervulina* induces a severe fatal relapse in chicks harbouring latent *P. gallinaceum* infections.

I wish to express my sincere thanks to Professor P.C.C. Garnham who supervised this work, and Dr R. Lainson who helped in identification, isolation of the coccidial parasites and the establishment of infection in clean laboratory-bred chicks.

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Parasitology (1961), **51**, 263
Printed in Great Britain

Trypanosomes of African fresh-water fish: an addendum

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(*Received* 26 *January* 1961)

In a paper recently published in *Parasitology* (Baker, 1960), I referred to the description of trypanosomes from the fish *Malapterurus electricus* and *Labeo macrostoma* by Rodhain (1908). Most regrettably, I was unaware until after my paper was printed of the existence of a later publication by Rodhain (1942) in which these trypanosomes were named *Trypanosoma malopteruri* (sic.) and *T. gandéi*, respectively. Rodhain's descriptions are rather brief, and it is difficult to compare them with those of earlier authors, which are often also lacking in detail: however, in the light of present knowledge of the morphological variability of these large trypanosomes and their wide host-ranges (in the few cases in which these are known), there seems to be no sure ground for regarding *T. malopteruri* and *T. gandéi* as valid species: possibly both are synonyms of *T. toddi* Bouet (1909), if it be assumed that Bouet saw only the larger forms of a pleomorphic species.

I can find no reference to subsequent publication of the name *T. nilotica* (or *niloticum*) Karam (1935), referred to briefly by Rodhain (1942), the original reference being in a thesis submitted to the University of Toulouse. Unless this thesis was actually published, this specific name must be regarded as a *nomen nudum*.

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Parasitology (1961), **51**, 265–267
Printed in Great Britain

A note on the behaviour of an avirulent strain of *Toxoplasma gondii* in some B-vitamin deficient chicks

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(*Received* 26 *August* 1960)

The following account describes experiments upon the behaviour of an avirulent strain of *Toxoplasma goudii* in chickens deficient in B-vitamins

MATERIALS AND METHODS

The chicks used in the study were either Rhode Island Reds or White Leghorns. One-day-old chicks were put on standard baby chick mash for 1 week before being put on the vitamin-deficient experimental diet. The chicks were kept on the experimental diet till they clearly manifested the characteristic symptoms of vitamin deficiency, which usually took about 4–5 weeks. The biotin-deficient diet and the pantothenic acid-deficient diet were compounded in the laboratory following the methods of Ott (1945) and Jukes & McElroy (1943) respectively. The control chicks in both cases were fed with normal chick mash supplemented with the B vitamin missing from the experimental diet. The nicotinic acid (niacin)-deficient diet and the riboflavin-deficient diet were supplied by Messrs Nutritional Biochemicals Corporation, Cleveland, U.S.A. These two diets had been prepared from their standard 'Vitamin B Complex Test Diet', supplemented by their 'Vitamin Diet Fortification Mixture' minus nicotinic acid and riboflavin respectively. The control birds were fed with the same diet supplemented with the vitamin missing from the deficient diets. The heat-labile vitamins deficient diet was prepared by autoclaving chick mash for 2 hr. each day on 3 consecutive days at 15 lb. pressure (120° C.) as adopted by Becker & Lawrence (1942). Normal chick mash was used as control diet.

When the characteristic symptoms of vitamin deficiency appeared, the experimental birds were infected intraperitoneally with 1 ml. of macerated mouse brain suspension containing cysts of the RB25 avirulent strain of *Toxoplasma*. This suspension was prepared by macerating, in 10 ml. of saline, the brains of three mice which had been previously infected with the RB25 strain of *Toxoplasma*. Each microscopic slide of this suspension contained about 3–4 cysts, giving an average of about 70 cysts per inoculum. Two birds from the same batch of chicks on control diet and six mice were also infected intraperitoneally with the same mouse brain suspension, each mouse getting half the infective dose given to the chicks. The infected birds were kept on the deficient diet for 2 weeks after infection, after which they were put back on the control diet supplemented with the vitamin missing from the deficient diet. At the end of 1 month, the control mice were

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sacrificed and their brains examined for cysts of *Toxoplasma*. If these were positive, the experimental chicks and the control chicks were sacrificed. Their brains were dissected out, macerated in saline, and the suspension from each of the birds injected intraperitoneally into six mice. These mice were sacrificed at the end of a month and their brains examined for cysts.

In addition, two chicks on normal diet supplemented with cod-liver oil, and two control chicks were infected intraperitoneally with avirulent *Toxoplasma*, at 3 weeks of age. They were maintained on the same diet till they were sacrificed at the end of a month and examined for the presence of *Toxoplasma*.

RESULTS

The results of the experiments on vitamin-deficient chicks are shown in Table 1. Altogether thirteen birds which had been made deficient in one vitamin or another and ten control birds were infected. All the control mice and chicks survived the infection and, when sacrificed, were found to harbour avirulent *Toxoplasma*. The biotin-, pantothenic acid-, and heat-labile vitamins-deficient chicks survived the

Table 1. *Number of each vitamin-deficient chicks infected*

Deficient vitamin	No. of vitamin-deficient chicks infected	Results
Biotin	2	All infected
Pantothenic acid	2	All infected
Nicotinic acid	4	One chick died on the 12th day. All infected
Riboflavin	3	One chick died on the 18th day. All infected
Heat-labile vitamins	2	All infected

infection and avirulent *Toxoplasma* were found in their brains. A chick from the nicotinic acid-deficient group and one from the riboflavin-deficient group died on the 12th and the 18th day respectively, but all these experimental birds also harboured avirulent *Toxoplasma* in their brains. The birds on cod-liver oil supplemented diet and their controls also harboured avirulent *Toxoplasm* in their brains.

DISCUSSION

Jones, Melton, Lunde, Eyles & Jacobs (1959) could not demonstrate differences in susceptibility to *Toxoplasma* and in the distribution of parasites in the tissues between folic acid-deficient chicks, vitamin B_{12}-deficient chicks and their respective controls. In the present study too, despite the small numbers involved, it was concluded that biotin-, pantothenic acid-, nicotinic acid-, riboflavin- and heat-labile vitamin deficiencies do not influence the susceptibility of the chicks to avirulent *Toxoplasma*. The death of one chick each from the nicotinic acid- and riboflavin-deficient chicks is considered to be due to the severity of the deficiency rather than

to acute toxoplasmosis. The administration of cod-liver oil to the normal diet similarly did not influence the susceptibility of the chicks to infection.

However, a difference was observed from the results reported by Jones *et al.* (1959). Repeatedly, they rarely recovered *Toxoplasma* 4 weeks or longer after infection from chicks which had been infected intravenously with *Toxoplasma* at 8 days or 6 weeks old. Although the age of most of the birds used in the present study was 5–6 weeks at the time of infection, *Toxoplasma* was isolated by mouse passage from the brains of twenty-five birds at the end of a month after infection. Of this number half were birds on a normal diet. Manwell, Coulston, Binckley & Jones (1945) also reported that *Toxoplasma* survived up to a maximum period of 206 days among seventeen birds, most of which were older than 8 weeks (some of them being even 3 months old) at the time of inoculation, two having been infected intraperitoneally, fourteen intracerebally, and one into the embryo. However they do not give any more details. No explanation can be given for the discrepancy between the results obtained in our study and those obtained by Jones *et al.* (1959), except to attribute it to the larger dose of *Toxoplasm* the birds in the present study would probably have received due to the fact they were inoculated with cysts and that different routes of infection were used in the two studies.

SUMMARY

No differences in susceptibility or parasite distribution of avirulent *Toxoplasma* was observed between biotin-, pantothenic acid-, nicotinic acid-, riboflavin- and heat-labile vitamins-deficient chicks and their controls. Ordinary diet supplemented with cod-liver oil did not have any effect either. Avirulent *Toxoplasma* were readily isolated from the brains of all the animals at the end of 1 month.

We are grateful to Professor P. C. C. Garnham for his interest.

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